Order Odonata

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Chapter Outline

INTRODUCTION

Systematic and Phylogenetic Relationships

Dragonflies belong to the superorder Odonatoptera, one of the oldest insect radiations to take flight, dating back at least to the early Carboniferous. This radiation includes the largest insect that ever lived, the griffenfly *Meganeuropsis permiana* Carpenter, 1939, with a wingspan of c. 70 cm. The radiation led to the rise of the order Odonata, with the oldest fossils dating back to the Permian. The present-day Odonata is regarded as a monophyletic group, which is divided into three suborders: Zygoptera or damselflies and Anisoptera or true dragonflies—each with approximately 3000 species—and a small suborder Anisozygoptera (damsel dragons) with four species. Unique features of odonates are the strongly modified larval labium and the mechanism of indirect sperm transfer (both described later), which requires a male copulatory organ at the second abdominal segment. Sperm must be transferred externally to this organ before copulation. During the insemination, the male holds the female with his abdominal appendages, behind the head (Anisoptera) or on the prothorax (Zygoptera), while the female bends the tip of her abdomen toward the secondary genitalia of the male, forming the well-known mating wheel of dragonflies.

In the past, wing venation was used as the main guide for classifying Odonata; but as similar characters evolved multiple times, this is often not a reliable indication of close relationships. Studies incorporating other morphological features, including those of larvae, have helped to overcome this (von Ellenrieder, 2002; Rehn, 2003; Fleck et al., 2008a), as have molecular studies (Bybee et al., 2008; Carle et al., 2008; Fleck et al., 2008b; Dumont et al., 2010). Molecular studies have in particular resulted in major changes in odonate taxonomy in recent years (Dijkstra and Kalkman, 2012). For Anisoptera we follow here the taxonomy proposed by Dijkstra et al. (2013); while for Zygoptera the taxonomy of Dijkstra et al. (2014) is used. The inferred phylogeny of extant Odonata is shown in Figure 35.1. A checklist of all dragonflies including synonyms and references is available on www.odonata.info.

Zygoptera

The adults (imagines) have a broad head with widely separated eyes and a slender abdomen. The fore and hind wings are similar in shape, and most species rest with their wings closed. The larvae have three (sometimes two) caudal gills for respiration, which can also be used as flippers for swimming. It is generally agreed that the suborder is monophyletic, and that the superfamily Lestoidea constitutes the sister group of the remaining 93% of the damselfly species. The monotypic family Hemiphlebiidae from southeastern Australia and Tasmania is the sister group of the three other lestoid families. Lestidae comprises 72% of the lestoids and, while monophyletic, its main genus *Lestes* Leach, 1815, is very heterogeneous and likely to be split in the future. While the 150 lestid species occupy mainly open, stagnant, and often temporary waters worldwide, the less than 60 other lestoids are localized in mostly mountain or forest streams. Synlestidae is found in eastern Australia, southern and central Africa, and the tropics of mainland Southeast Asia, while Perilestidae is restricted to the Neotropics.

Platystictoidea with its sole family Platystictidae is the sister group of all Zygoptera excluding Lestoidea. The group is confined to the wettest tropics, being notably absent from Africa and Madagascar. While it is also present in Central and northern South America, 80% of the species occur from Sri Lanka and India to New Guinea. Currently the over 220 species are placed in only eight genera, a higher ratio than in any other family. This is due to the highly polyphyletic nature of the two main genera, *Protosticta* Selys, 1885, and *Drepanosticta* Laidlaw, 1917, which will undoubtedly be split up in the near future.

About 58% of all damselfly species belong to the superfamily Coenagrionoidea, which includes three families. Isostictidae is the smallest, containing less than 2% of all damselfly species, all of which are confined to Australia, New Guinea, New Caledonia, and neighboring
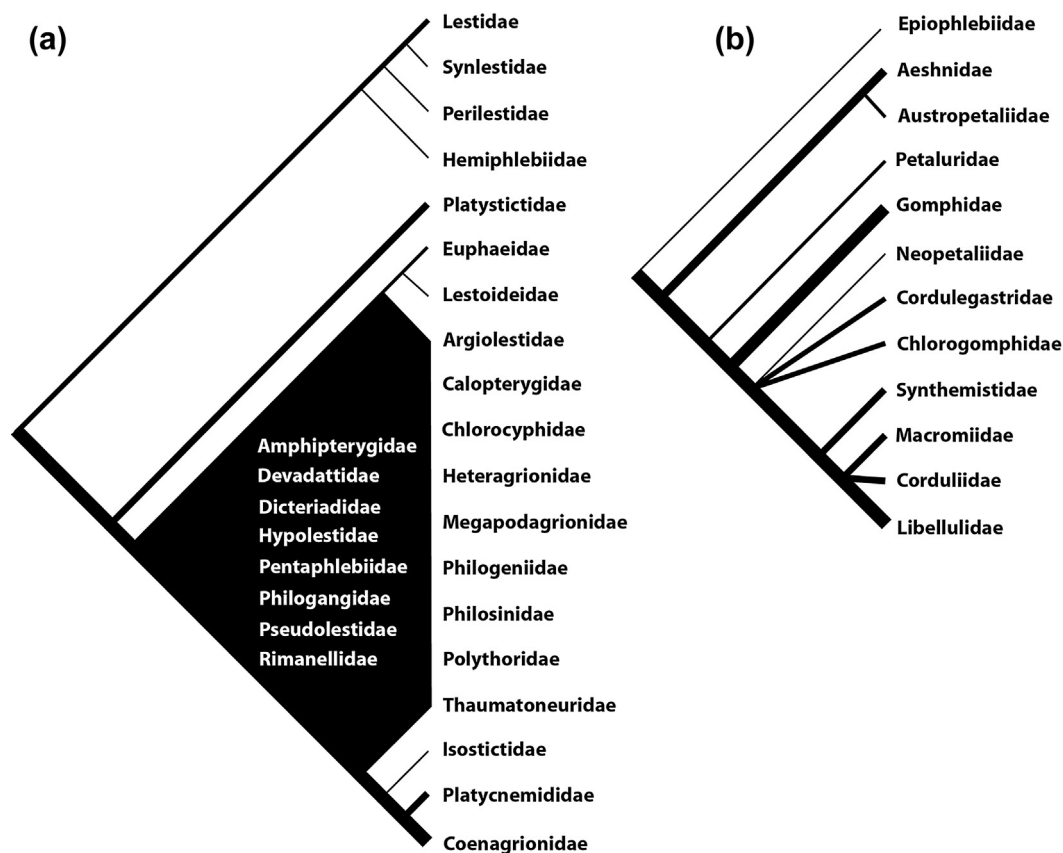
(a)

Lestidae
Synlestidae
Perilestidae
Hemiphlebiidae
Platystictidae
Euphaeidae
Lestoideidae
Argiolestidae
Calopterygidae
Chlorocyphidae
Heteragrionidae
Megapodagrionidae
Philogeniidae
Philosinidae
Polythoridae
Thaumatoneuridae
Isostictidae
Platycnemididae
Coenagrionidae

Amphipterygidae
Devadattidae
Dicteriadidae
Hypolestidae
Pentaphlebiidae
Philogangidae
Pseudolestidae
Rimanellidae

(b)

Epiophlebiidae
Aeshnidae
Austropetaliidae
Petaluridae
Gomphidae
Neopetaliidae
Cordulegastridae
Chlorogomphidae
Synthemistidae
Macromiidae
Corduliidae
Libellulidae

FIGURE 35.1 Inferred phylogeny of families of: (a) Zygoptera and (b) Anisozygoptera (Epiophlebiidae) and Anisoptera. Line thickness is indicative of species diversity. The relationships of most families within Zygoptera are unresolved, and this polytomy is here depicted as a paraphyletic assemblage. The numerous monogeneric families within this polytomy are listed to the left. Genera *incertae sedis* not shown. *Figure by VK and KD.*

islands. Platycnemididae is restricted to the Old World and contains over 400 species, most of which are confined to streams and rivers. One of its subfamilies (Disparoneurinae) comprises all Old World species of the former family Protoneuridae. Coenagrionidae is the largest damselfly family with over 1200 species. The family includes two large lineages that are referred to as the core and the ridge-faced Coenagrionidae, each with about 600 species. Although both groups are found worldwide, a relatively high proportion of the ridge-faced species occurs in tropical forests. In tropical America, they constitute two-thirds of the damselfly species, including all the New World species of the former families Protoneuridae and Pseudostigmatidae. The core Coenagrionidae tend to dominate in more open and temperate areas, outnumbering the ridge-faced group in Africa, the Palaearctic, and Australia by about four to one. This group includes many well-known genera such as *Coenagrion* Kirby, 1890, *Enallagma* Charpentier, 1840, and *Ischnura* Charpentier, 1840. In the Oriental and Pacific regions, the two groups are more equally balanced, with about 40% of the species being ridge-faced, large genera being *Ceriagrion* Selys, 1876, and *Teinobasis* Kirby, 1890.

The superfamily name Calopterygoidea has been used for a very diverse assemblage of mostly densely veined damselflies constituting 27% of the total damselfly diversity. While the other superfamilies are quite well defined, the remaining families are grouped together without much evidence for their monophyly. Calopterygoidea may ultimately prove polyphyletic, requiring the creation of further superfamilies. With almost a quarter of the species, Calopterygidae is the largest and most widespread family within Calopterygoidea, although it is absent from Australia. Four long-recognized smaller families are each morphologically very distinctive and clearly monophyletic, being largely confined to streams and rivers in the Old (Chlorocyphidae and Euphaeidae) and New World tropics (Dicteriadidae and Polythoridae).

The taxonomy of the remainder of the Calopterygoidea is problematic, and during the past decades most genera have been classified as either Amphipterygidae or Megapodagrionidae. Molecular work has resulted in the creation and reinstatement of many additional families, but their relationships are poorly understood. Seven genera have been considered part of Amphipterygidae, but molecular analyses have shown them to be

polyphyletic, and they are currently placed in six families. Of these, Amphipterygidae (Central America), Devadattidae (Southeast Asia), Pentaphlebiidae (Central Africa), Rimanellidae (South America), and Philogangidae (mainland tropical Asia) each contains only one genus, while the Australian Lestoideidae contains two. Together, these families include only 25 species.

The heterogeneity of Megapodagrionidae has long been recognized. Based on the shape of the larval gills, they can be divided in four groups: Argiolestidae with long triquetral gills (Eastern Hemisphere), the Asian Philosinidae in which the lateral gills form a tube, and the South American Megapodagrionidae (in the strict sense) with flat horizontal gills. The remaining genera all have saccoid larval gills. Based mainly on molecular evidence, these can be subdivided into the tropical American Heteragrionidae, Hypolestidae, and Philogeniidae; while the Pseudolestidae is endemic to the Chinese island Hainan, and the Thaumatoneuridae contains two Central American and southern Asian genera. Even with the addition of these families, the position of 10 genera remains uncertain. It is likely that further work will show that these constitute seven additional families.

Anisozygoptera

The suborder contains only the family Epiophlebiidae, with its single genus *Epiophlebia* Calvert, 1913. Only four elusive species are known from Japan, the eastern Himalayas, and two recently described species from China. The suborder is sometimes combined with Anisoptera to form the suborder Epiprocta. They resemble Anisoptera in most respects but have stalked wings, and they close their wings when at rest. Their larvae live in cold running water. They lack caudal gills and, like Anisoptera, absorb oxygen through gills in the rectum.

Anisoptera

The anisopteran imagines are on average larger and more robust than those belonging to Zygoptera. Their hind wings are distinctly broader at the base than the fore wings, and in most families the eyes touch on top of the head. At rest most species spread their wings. The larvae are typically also sturdier and lack caudal gills. There is a general agreement that the suborder is monophyletic and can be divided into five superfamilies. The most comprehensive analysis of odonate phylogeny to date (Bybee et al., 2008) places Aeshnoidea as the sister group of all other Anisoptera, followed by Petaluroidea, Gomphoidea, Cordulegastroidea, and Libelluloidea.

The monophyly of Aeshnoidea and its two families, Aeshnidae and Austropetaliidae, is well supported. Aeshnidae is a large family occurring worldwide. A morphological phylogeny found little support for most recognized subfamilies (von Ellenrieder, 2002), some of which are

occasionally treated as families. Austropetaliidae shows a relict distribution with two genera restricted to southeastern Australia and Tasmania and two others to southern Chile and adjacent Argentina. Petaluridae, the sole family of the well-defined superfamily Petaluroidea, includes only 10 relict species occurring in North America, Japan, Australia, New Zealand, and Chile.

The Gomphidae (Gomphoidea) comprise nearly one-third of all anisopteran species. Carle (1986) recognized eight subfamilies, of which Lindeniinae is occasionally treated as a family—Lindeniidae. However, with no extensive molecular phylogeny available, the validity of any classification remains untested. Moreover, for the sake of stability, it seems best to limit any further subdivision to the subfamily level at most. The family is the third largest within the order and is virtually cosmopolitan.

The two largest families within the superfamily Cordulegastroidea, the largely Oriental Chlorogomphidae and the largely Holarctic Cordulegastridae, both include about 50 species. Both families have only three widely accepted genera each. Many additional genera have, however, been proposed, and proper study is required to understand their validity. The third family, Neopetaliidae, is geographically highly isolated and monotypic since all genera except the Chilean *Neopetalia* Cowley, 1934, were transferred to the distantly related Austropetaliidae.

The monophyly of Libelluloidea, comprising almost half of all anisopterans, and three of its families, Libellulidae, Corduliidae, and Macromiidae, is well supported. Libellulidae, containing over 70% of libelluloid species, is the most species-rich family of Anisoptera and occurs worldwide. Although a few clusters of related genera have been identified, no overall divisions within Libellulidae are apparent, and thus traditionally recognized subfamilies seem largely invalid. Macromiidae is dominated by two huge genera. Over 35 African species belong to *Phyllomacromia* Selys, 1878, and nearly 80 to *Macromia* Rambur, 1842, occurring from North America across Eurasia to northern Australia. Their classification may require reevaluation, especially in relation to the two remaining genera: the North American *Didymops* Rambur, 1842, and the Asian *Epophthalmia* Burmeister, 1839. Corduliidae consists of mostly Holarctic genera, a few Neotropical groups, and the predominantly Australasian group around *Hemicordulia* Selys, 1870. Synthemistidae is a small family of 46 species divided over eight genera and is found in Australia, New Caledonia, and the Papuan region. The remaining 21 genera were traditionally placed in Corduliidae. An extensive molecular analysis showed these to fall outside Corduliidae and to be nearer to Synthemistidae (Ware et al., 2007). It is, however, unclear if they form a monophyletic group or are better being placed in several small families. For the moment they are regarded as *incertae sedis*. These genera occur predominately in Australia and tropical Asia and America; none are known from North America.

Species Numbers

Odonata contained 5956 described species as of 2010 (39 families, 659 genera), of which 2942 belong to the suborder Zygoptera (309 genera, 27 families), 3012 to the Anisoptera (348 genera, 11 families) and 2 to the Anisozygoptera (1 family, 1 genus; plus 2 spp. which were described in 2012). Table 35.1 provides the number of genera and species for each family and biogeographical region. It is estimated that between 1000 and 1500 species still await description. If true, the actual number of extant species will be between 7000 and 7500. Since 1970, nearly 40 species have been described annually, and with an undiminished rate of description an estimated 95% of all species will be described in 2030. The Oriental, Australasian,

and especially the Neotropical regions hold the highest number of undescribed species. About 250 species were described between 2006 and 2010, nearly all from tropical regions, with the highest contributions from the Neotropical (43%), Oriental (28%), and Australasian regions (19%, nearly all from New Guinea, Moluccas and Sulawesi). Three-fifths belonged to only three families, Coenagrionidae (85 species), Libellulidae (37), and Platystictidae (27). The first two constitute the largest odonate families and are relatively well known, as most species are conspicuous and many favor open habitats, although in absolute numbers they still represent a large proportion of species to be described. Argiolestidae, Platystictidae, and Gomphidae are believed to hold relatively many undescribed

TABLE 35.1 Number of Genera (G) and Species (S) per Biogeographic Region

Taxon	Oriental G	Oriental S	Neotropical G	Neotropical S	Australasian G	Australasian S	Afrotropical G	Afrotropical S	Palaearctic G	Palaearctic S	Nearctic G	Nearctic S	Pacific G	Pacific S	World G	World S
Zygoptera																
Lestoidea																
Hemiphlebiidae					1	1									1	1
Lestidae	5	40	2	42	3	29	1	17	4	18	2	18	3	3	9	151
Perilestidae			2	19											2	19
Synlestidae	2	18	1	1	3	8	3	11	2	6					9	39
Platystictoidea																
Platystictidae	7	136	1	43	2	44					1	1	1	1	8	224
Calopterygoidea																
Amphipterygidae			1	4											1	4
Argiolestidae	2	10			11	73	3	19					4	6	20	108
Calopterygidae	12	66	5	68	1	5	3	20	8	37	3	8			21	185
Chlorocyphidae	15	86			4	17	3	42	4	3					20	144
Devadattidae	1	6													1	6
Dicteriadidae			2	2											2	2
Euphaeidae	8	65			1	1			5	11					9	68
Heteragrionidae			2	51											2	51
Hypolestidae			1	2											1	2
Lestoideidae					2	9									2	9
Megapodagrionidae			3	29											3	29
Pentaphlebiidae							1	2							1	2
Philogangidae	1	4							1	2					1	4
Philogeniidae			2	39											2	39
Philosinidae	2	12													2	12

(Continued)

TABLE 35.1 Number of Genera (G) and Species (S) per Biogeographic Region—cont'd

Taxon	Oriental G	S	Neotropical G	S	Australasian G	S	Afrotropical G	S	Palaearctic G	S	Nearctic G	S	Pacific G	S	World G	S
Polythoridae			7	59											7	59
Pseudolestidae	1	1													1	1
Rimanellidae			1	1											1	1
Thaumatoneuridae			2	5											2	30
Incertae sedis	7	25	4	11			3	19	3	9					14	61
Coenagrionoidea																
Coenagrionidae	20	193	69	554	21	152	18	202	12	96	16	103	12	91	114	1266
Isostictidae					11	41							1	5	12	46
Platycnemididae	9	199			16	122	13	70	6	22					42	404
Anisozygoptera																
Epiophlebioidea																
Epiophlebiidae	1	1							1	1					1	2
Anisoptera																
Aeshnoidea																
Aeshnidae	18	149	15	129	19	78	8	44	13	58	13	40	6	13	51	456
Austropetaliidae			2	7	2	4									4	11
Petaluroidea																
Petaluridae			1	1	2	6			1	1	2	2			5	10
Gomphoidea																
Gomphidae	42	364	26	277	9	42	19	152	33	127	14	101			87	980
Cordulegastroidea																
Chlorogomphidae	3	46							1	5					3	47
Cordulegastridae	3	23	1	1					3	18	1	10			3	46
Neopetaliidae			1	1											1	1
Libelluloidea																
Corduliidae	5	23	5	20	6	33	2	6	4	18	7	51	3	12	20	154
Libellulidae	56	192	45	354	45	184	50	251	31	120	26	105	16	31	142	1037
Macromiidae	2	50	1	2	2	17	1	37	2	7	2	10			4	125
Synthemistidae					8	37							1	9	8	46
Incertae sedis	2	37	4	24	10	21	4	15	2	2					20	99
Total	234	1746	206	1746	179	924	133	907	135	561	87	449	47	171	659	5956
Undescribed spp.	300–400		400–500		175–250		100–125		75–100		5–10		30–40		1085–1425	

Information on the number of odonate species and their distribution is derived from the global species database Odonata (Tol van, 2012). The list, first published by Kalkman et al. (2008), was updated to include all species described up to 2010. Subspecies were not considered. Since species and genera may occur in more than one biogeographic region, totals may not fit.

species. They are typically inconspicuous odonates with small ranges, often confined to seepages or small runnels in tropical forest.

GENERAL BIOLOGY

External Features of the Larva

Dragonfly larvae have principally the same anatomy as adults, in that the head carries the eyes, antennae, and mouthparts; the thorax has three pairs of legs and wing sheets in older instars; and 10 abdominal segments are present (Figure 35.2). We base our descriptions here mainly on Tillyard (1917).

The head bears the compound eyes, three ocelli (which may have mainly a function in light/dark perception), and the antennae. The large compound eyes are built of numerous ommatidia, whose numbers increase during the larval development. Early instar larvae have only seven ommatidia per eye; only aeshnids and lestids have more. Also in later instars, eye size varies significantly. Members of the family Aeshnidae, particularly the genus *Anax* Leach, 1815, have huge eyes, whereas some Libellulidae, for instance of the genus *Libellula* Linnaeus, 1758 have comparatively small eyes. The antennae bear mechanoreceptors, which are used for tactile perception of prey and also as olfactory receptors. They usually have six to seven segments of similar size. Exceptions include Calopterygidae and Chlorocyphidae, whose basal antennal segment is usually much longer than the others. Gomphidae only have four antennal segments,

the third of which is enlarged. The reason for having different-sized antennal segments is unknown. In gomphids, however, the more compact antennae may be an adaptation to the larva's burrowing way of life.

A unique feature of dragonfly larvae, in which they differ to a great extent from adults, is their ejectable labium (Figure 35.3). The labium serves as the principal apparatus for capturing prey and allows an extension of the area onto which prey can be fixed. It consists of four moveable elements: the postmentum, the prementum, and two labial
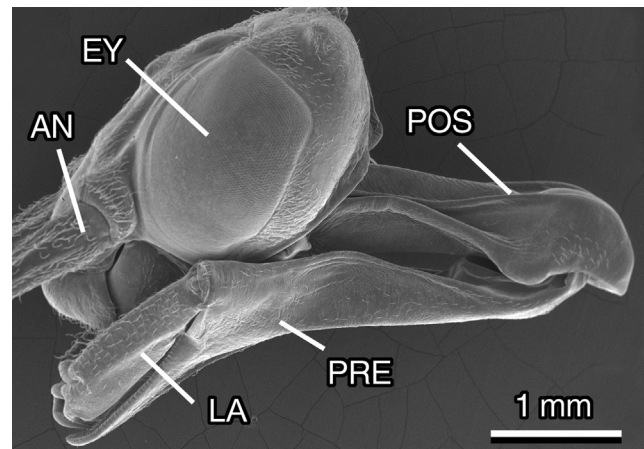

FIGURE 35.3 SEM of the head of *Calopteryx splendens* (Harris, 1780), showing the postmentum (POS), prementum (PRE), and labial palps (LA). The eyes (EY) and base of antennae (AN) are also visible. *Photo by SG.*
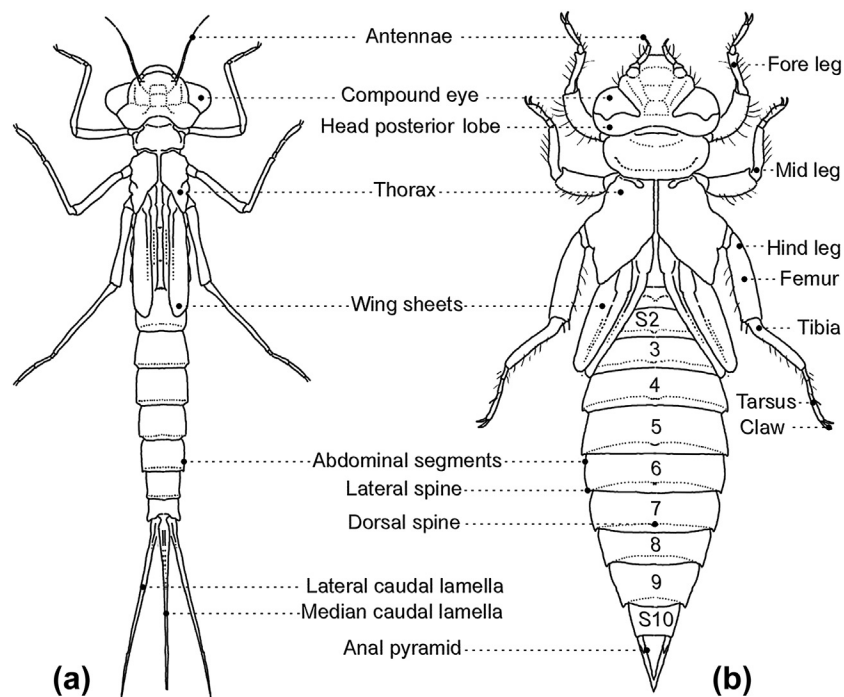

FIGURE 35.2 External features of Odonata larvae. (a) Zygoptera and (b) Anisoptera. *Drawings by Ole Müller.*

palps. In a resting position, the labium is folded backward under the body. The strike of the labium is mediated by hydraulic pressure, initiated by contraction of abdominal muscles and closure of the anal pyramid (anal opening in Zygoptera). While building up pressure, the labium is locked into place by muscles within the labium. Relaxation of the muscles induces an explosive protraction, which lasts between 15 and 40 ms. The retraction of the labium is mainly achieved by muscular contraction. The labium (including the labial palps) is shovel or spoon shaped, covering parts of the face as in Cordulegastroidea and Libelluloidea, or more forceps-like and not covering the face, as in all other odonates (Figure 35.4(a) and (b)). A spoon-shaped labium may provide the larva with a greater catchment volume, allowing it to catch relatively small prey compared with its body size. This is supported by long setae forming a lattice that locks the prey in the labium. The forceps-like labium is useful for capturing larger prey. In addition, the length of the labium varies; in Gomphidae and some others, it is very compact, only extending posteriorly to the first pair of legs. These are often bottom dwellers and/or use mechanoreceptors for prey detection. By contrast, in the species belonging to the genera *Lestes* Leach, 1815, and *Anax*, which live among vegetation and mainly capture visually detected prey, the labium reaches as far back as the last pair of legs.

The six legs and, in later instars, the wing sheets insert into the thorax. The legs consist of two small basal segments (coxa and trochanter), two longer elements (femur and tibia), and three very small segments forming the foot (tarsus), which terminates in two claws. The legs vary in shape between families according to microhabitat occupancy (see below) and life style.

The abdomen has 10 segments (often abbreviated as S1, S2, etc., also in adults). In Anisoptera the 10th segment bears a so-called anal pyramid formed from the epi- and paraprocts and the cerci. In Zygoptera, by contrast, the epi- and paraprocts form three caudal appendages, while the cerci are reduced (as is the epiproct in Chlorocyphidae). The abdomen may be cylindrical in cross-section and rather elongated, as in most Zygoptera, as well as in the Aeshnidae, Cordulegastridae, and some Gomphidae. In many Gomphidae, Macromiidae, and Corduliidae, it may be dorsoventrally flattened and stout and even rounded in dorsal view. The shape of the abdomen is associated with the microhabitat occupancy, as described below.

External Features of the Imago

Imagines are sectioned into a head, thorax, and abdomen, and they have two pairs of wings formed by a network of stiffer veins and a flexible (mostly transparent) membrane.
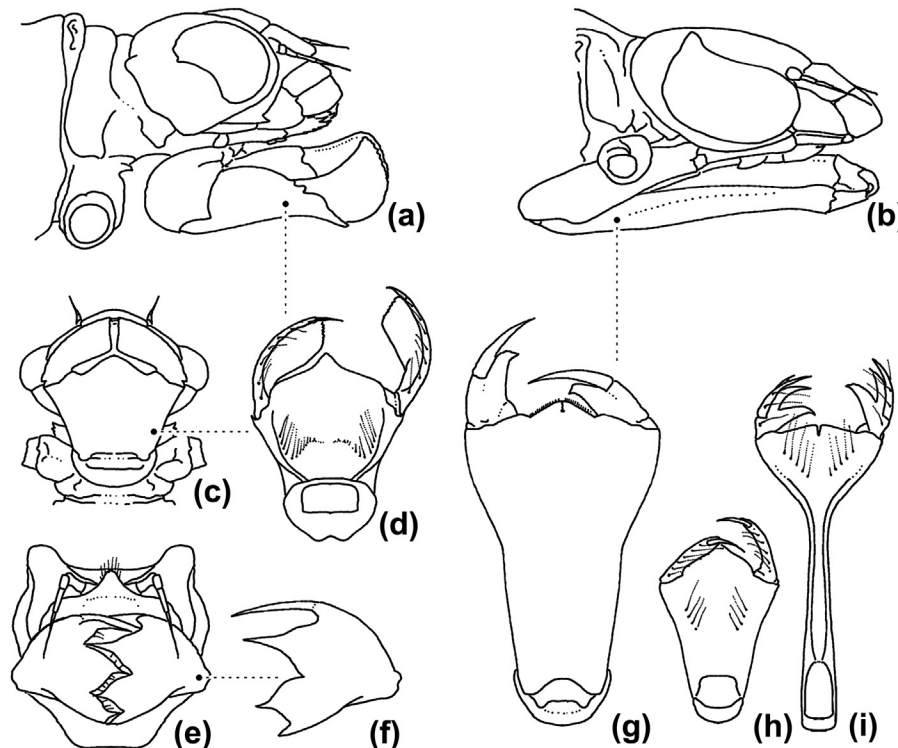

FIGURE 35.4   The labium of odonate larvae: a unique foraging organ. (a) Head with spoon-shaped labium in lateral view; (b) flat labium in lateral view; (c–f) structures of spoon-shaped labium; (c, d) labium of Libellulidae in dorsal and ventral view; (e, f) labium with deeply crenated palpae as in Cordulegastridae and Macromiidae in frontal view and one palpus enlarged; (g–i) variations of flat labium (g) long mentum of *Anax*; (h) short mentum of *Coenagrion*; (i) long mentum of *Lestes. Drawings by Ole Müller.*

Zygoptera and Anisoptera differ in the shape of the hind wings as well as in the arrangement of the compound eyes on the head (Figure 35.5(a) and (c)).

The head capsule bears the mouth and most of the major sensory organs for orientation. The globular compound eyes of Anisoptera cover a major part of the head and touch on top of the head in most families. In Zygoptera the eyes are located on the sides and are widely separated. Three singular ocelli on the forehead have a function in flight orientation. The link between the head and the prothorax is

FIGURE 35.5   External features of Odonata imagines. (a) Dorsal view of a Zygoptera (Coenagrionidae); (b) last segments of female Zygoptera abdomen in lateral view showing the ovipositor; (c) dorsal view of an Anisoptera (Libellulidae); (d) head enlarged in lateral view; (e) last segments of male Anisoptera abdomen (Gomphidae) showing appendages and foliation; and (f) secondary copulation organ of a male (g) Anisoptera (Macromiidae) in lateral view. *Drawings by Ole Müller.*

articulate and fragile, allowing the entire head to move so that in flight it can be used as a kind of gravity organ. However, when the dragonfly catches prey, the head is fixed by a unique arrester system (see below) to increase the mechanical stability of the head. The antennae are thread-like, very short, and divided into four to seven segments. The mouth is situated on the underside and consists of several mouthparts as named in Figure 35.5(d).

The thorax consists of three segments. The prothorax carries the front legs but no wings. This differs from some Palaeozoic dragonflies, which had small wing-like structures on the prothorax as well. The prothorax of damselfly females often has species-specific dorsal structures that may guide or fit the male appendices. The other two thoracic segments of both genders are fused, forming the synthorax, which carries the middle and hind legs and both pairs of wings.

The elongate wings are usually transparent between the veins but can also be partly colored. Anisopteran hind wings are broadest close to the base, whereas hind and fore wings are similar in shape and broadest in the outer third of their length in zygopterans. In some Libellulidae the hind wing base may be as broad as half the length of the abdomen. The wing veins form a network of principal, cross-, and other veins. Characteristic of odonate wings is the discoidal cell in the basal half of the wing, which is triangular in most dragonflies and quadrangular in damselflies. In most odonate families a pterostigma—a thicker and pigmented wing cell—is present at the anterior margin; it may reduce self-excited vibrations in the wing. The nodus is a unique feature of extant Odonata and may permit elastic tension/flexion of the wing's leading edge.

The imago has only limited use of the legs for locomotion. Their main function is in prey capture and handling; they are spread out, forming a "basket" during flight. Very long spines at femur and tibia enhance this function. The males also use the legs for grasping females and repelling rivals. Finally, the legs are used to cling to vegetation and other structures when resting or perching.

The abdomen is long and cylindrical in many species but relatively short and broad in many Libellulidae. In many Gomphidae and female Libellulidae, S8 and sometimes adjacent segments are often expanded with so-called foliations. In the Gomphidae these membranous structures appear like empennages, but their function is not yet understood. In males, the underside of S2 and S3 bear the secondary genitalia, which include additional structures (anterior lamina, hamuli, posterior lamina). In females of Zygoptera and some of the less derived Anisoptera (including Aeshnidae), the underside of S8 and S9 bear the strong ovipositor needed to deposit the eggs in plant tissues. In the two most species-rich groups of Anisoptera, the Gomphidae and Libelluloidea, the egg-laying apparatus is reduced to a spout, basket, or a pair of flaps. In males the abdomen terminates in upper and lower appendages that are used for seizing females during mating.

Size

Extant Odonata are not as large as their gigantic precursors (see above), but are still among the largest insects (Wilson, 2009). The zygopteran *Megaloprepus caerulatus* (Drury, 1782), has a wingspan of up to 19 cm and a body length of over 12 cm. Even longer are some species of *Mecistogaster* Rambur, 1842, that may reach 15 cm but have shorter wings. Anisoptera do not match these measurements, the largest having a wingspan of up to 16 cm and a body length of up to 12.5 cm, but they are much more massive than any Zygoptera. Species like *Tetracanthagyna plagiata* (Waterhouse, 1877), from Borneo together with some large *Anax* and *Petalura* Leach, 1815, species should, therefore, be regarded as the largest odonates. By contrast, the smallest odonates have wingspans and body lengths below 2 cm, for instance, damselflies of the Old World genus *Agriocnemis* Selys, 1877.

Egg Structure

Eggs vary from spheroid to spindle shaped, the largest reaching ~2 mm in length, while the majority are <0.5 mm in diameter (Corbet, 1999, p. 44). Most Zygoptera and Aeshnidae deposit their eggs in living or decaying plant tissue, while some members of this group choose more exotic substrates, e.g., soft stone in *Coenagriocnemis reuniensis* (Fraser, 1957). Species using this endophytic oviposition strategy (see below) have longer, in some cases bottle-shaped, eggs (Figure 35.6(h)) and use an ovipositor to make an incision in the substrate before inserting the egg. All other species employ exophytic oviposition, and their eggs are normally smaller and rounder in shape (Figure 35.6(i)) (Trueman, 1990; Corbet, 1999, p. 45). The eggshell consists of three layers, the vitelline envelope being the innermost one (Figure 35.6(f)). This layer is thick in species with overwintering eggs, e.g., *Sympetrum sanguineum* (Müller, 1764), but very thin in species where the eggs have direct development, like *Orthetrum cancellatum* (Linnaeus, 1758), (Sahlén, 1995). The vitelline envelope is believed to regulate the water balance of the egg. Outside the vitelline envelope lies the endochorion, which is multilayered, thicker in endophytic eggs, and sometimes very thin in exophytic ones. This layer is in turn covered by the flexible and elastic exochorion (Figure 35.6(d,f) and (g)). The elasticity is important when an egg is inserted into plant tissue, but in exophytic species this layer often appears like jelly, expanding when coming in contact with water at oviposition and thus anchoring the egg to the substrate or attaching particles to the egg surface as camouflage. The exochorion appears as thin, thread-like structures embedded in a matrix in endophytic species (Figure 35.6(e) and (f)) (Sahlén, 1995). At one end of the egg, micropyles through which sperm cells enter
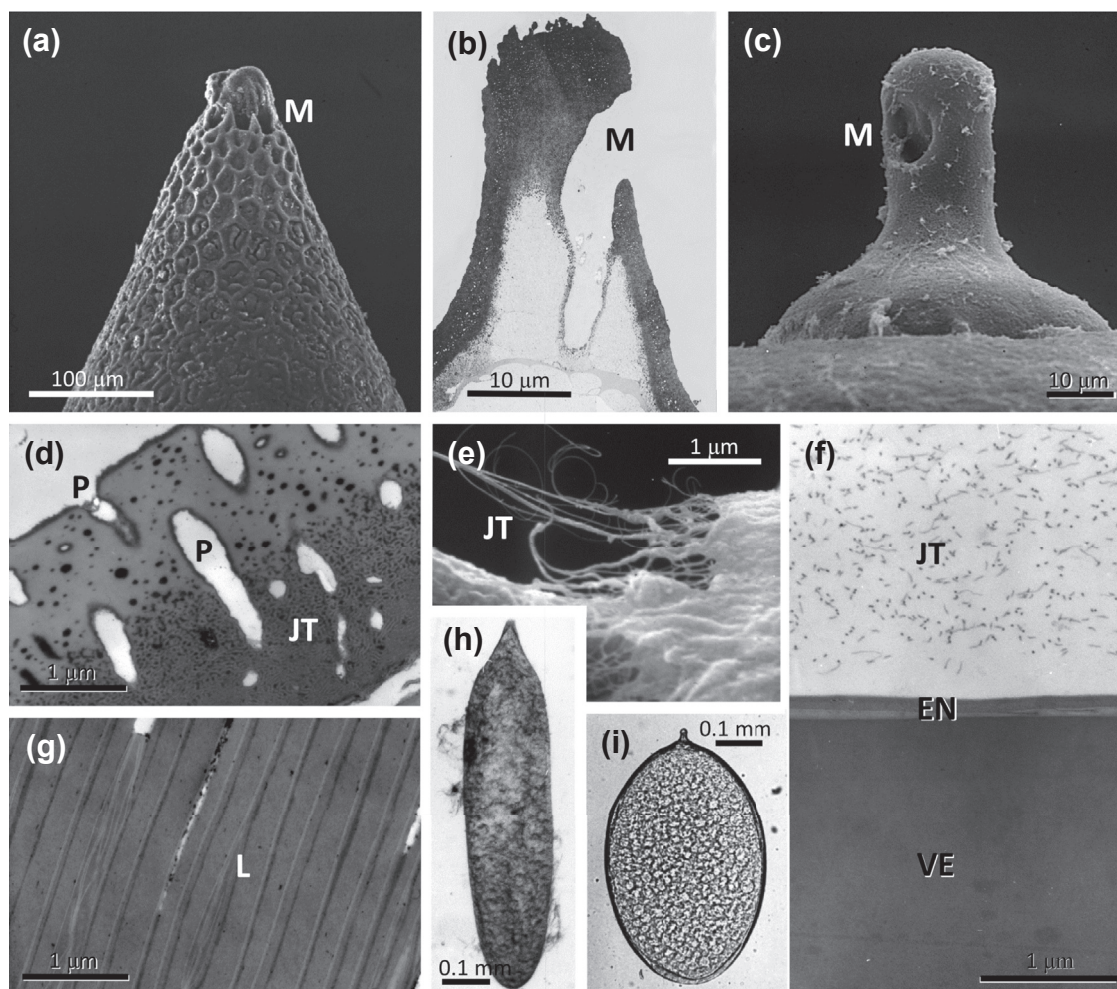
FIGURE 35.6 Eggs and egg shell details: (a) anterior end of endophytic eggshell in *Aeshna juncea* (Linnaeus, 1758); (b) anterior end of exophytic eggshell in *Somatochlora metallica* (Vander Linden, 1825), in cross section and (c) lateral view; (d) exochorion of *A. juncea* in cross-section; (e) jelly strands of *S. metallica*; (f) cross-section of eggshell in *Orthetrum cancellatum* (Linnaeus, 1758); (g) endochorion of *A. juncea* in cross-section; (h) egg of *Ischnura elegans* (Vander Linden, 1820); and (i) egg of *Somatochlora metallica* (Vander Linden, 1825) (all new or adapted originals). EN, endochorion; JT, exochorionic jelly threads; L, lamellar layers; M, micropyle; P, exochorionic pores; VE, vitelline envelope. *Photos by GS.*

at fertilization sit on a conical/rounded projection. They are numerous (up to 14) in Petaluridae, becoming gradually fewer in the more modern families, with only two in Libellulidae and some Corduliidae (Figure 35.6(a)–(c)). The projection with micropyles is more stable than the rest of the exochorion and never covered in jelly (Corbet, 1999, pp. 45–46). Some species have special structures on the egg adapting them to a certain life mode. A few examples are strands of jelly in *Ictinogomphus rapax* (Rambur, 1842), to anchor the egg, a second type of jelly binding a whole egg batch together into a long egg string in *Epitheca* Burmeister, 1839 spp., and even plastron respiration is reported from a few species, for instance *Brachythemis lacustris* (Kirby, 1889). The variation in external egg morphology is large in exophytic species, whereas the endophytic ones seem much more uniform (Corbet, 1999, pp. 46–50).

Ultrastructures

Dragonflies display a number of ultrastructural features, which are partially unique to this group of aquatic insects and/or possess fascinating properties. In this subsection we provide information about a few such structures.

Wing Structures

A dragonfly wing consists of a three-dimensional skeletal network of relatively hard longitudinal veins, which are interconnected through thin membranous areas called cells. Previous studies on the functional morphology of odonate wings have shown that camber and angle of attack are automatically maintained under aerodynamic load by a set of internal mechanisms including vein pattern, vein curvature, and type of joints between cross- and longitudinal veins. Although more than six different kinds of crossvein
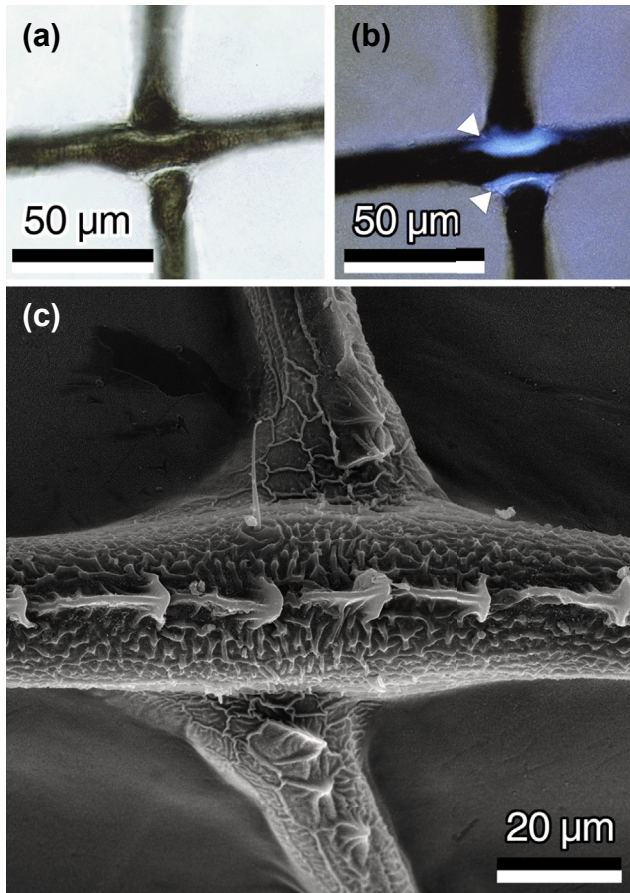
FIGURE 35.7 Wing vein articulations in *Enallagma cyathigerum* (Charpentier, 1840), supplemented with resilin, a rubberlike protein. (a) Bright-field light microscopy; (b) fluorescence microscopy; areas containing resilin (white arrowheads) are visible in UV wavelengths but not in bright-field light microscopy; and (c) typical mobile wing vein joint depicted with a scanning electron microscope (SEM). *Photos by SG.*

junctions to longitudinal veins are known, these junctions can be divided into two main types: immobile and mobile. The mobile vein joints contain resilin, a rubberlike protein that is responsible for elastic energy storage during deformations (Figure 35.7) (Gorb, 1999). Presumably, such joints are essential to the highly maneuverable flight of odonates, especially under conditions where unstable wind pulses act on the flying insect.

Coloration

Odonata demonstrate a wide variety of color patterns, which depend not only on pigments but also on a variety of physical mechanisms. Such colors are produced by light interference in thin external cuticle layers that are superimposed upon a dark-colored underlying pigment (Figure 35.8(a, c)). Typical metallic colors generated by such a mechanism are emerald green, bronze green, copper, blue, violet, and purple (Tillyard,

1917). Epidermal (subcuticular) coloration relies on granules located in the epidermal cells, such as those described as blue or green abdominal spots in species of the genera *Anax* and *Enallagma* (Prum et al., 2004).

Another form of coloration depends on the crystalline wax coverage of the cuticle surface. This is a kind of supracuticular pigment, which is often called pruinescence or pruinosity. An example of this is the whitish lantern of *Calopteryx* males. This ventral part of the abdomen, which is used in courtship displays, is covered with a thick layer of long, densely packed and often randomly oriented wax crystals (Figure 35.8(b)). These structures cause strong light scattering yielding a whitish color. These in combination with colors of the underlying cuticle (yellow, red, black) can generate new shades of, for example, orange, purple, or blue (Kuitunen and Gorb, 2011), as is especially notable in many genera of Libellulidae. Cuticle coverage by wax crystals is known in most adult dragonflies. In fact, almost the entire body of the imago except the eyes and ocelli is covered with such structures. These are responsible for trapping air and reducing the wettability of the body surface (Figure 35.8(d)). The body surface of the larva contains no such coverage.

Cuticula

The dragonfly cuticle is similar to that of other insects in being a stratified material penetrated by arrays of pore canals (Figure 35.9(g)). Trachea, which are involved in gas transport and respiration, also have a cuticular origin. Their reticulate membraneous part is reinforced by circular stiffening called taenidia (Figure 35.9(h)). Stiff parts of the body cuticle called sclerites are interconnected through arthrodial membranes, which in adult dragonflies have a very peculiar surface structure consisting of folds (Figure 35.9(b) and (c)) that can unfold under tension. One of the functions of such a specialized surface pattern is to make the membrane extremely stretchable, which may be essential in very mobile joints such as the head-neck articulation in adult dragonflies. The mobility of the head is important to its function as a kind of gravity detector organ in flight. However, such mobility entails a rather low mechanical stability, which necessitates reinforcement provided by the so-called head arrester.

Head Arrester System

The head-arrester or fixation system of the head in adult Odonata is unique among insects. This system involves organs in the head and prothorax segments. It consists of an exoskeleton-muscle apparatus that sets the arrester parts in motion. The parts comprise formations covered with fields of microtrichia on the rear surface of the head (Figure 35.9(f)) and postcervical sclerites of the prothorax (Figure
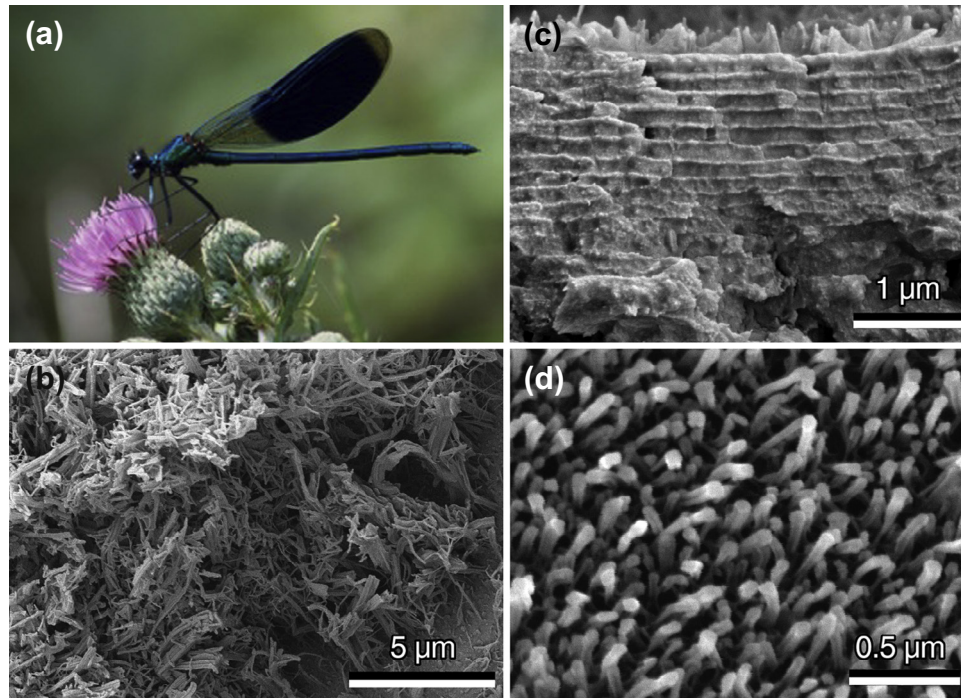
FIGURE 35.8   Ultrastructural basis for coloration and reduced wettability (SEM images). (a) A fully colored male of *Calopteryx splendens*; (b) a thick cover of crystalline wax on the lantern (ventral surface of the abdomen tip) used in courtship displays in an old male of *C. splendens*; (c) fracture of the cuticle of the 7th abdominal segment of a *C. splendens* male, exocuticle layers are responsible for light interference causing metallic blue coloration *(From Kuitunen and Gorb (2011).)*; and (d) ventral forewing surface in *Coenagrion puella* (Linnaeus, 1758). Showing an array of tiny wax crystals responsible for trapping air when ovipositing under water and reducing wettability of the wing surface. *Photos: (a) by FS, all others by SG.*

35.9(d) and (e)), which connect to each other like Velcro if stability is required. The arrester immobilizes the head during feeding or when the dragonfly is in tandem flight. Thus, it may serve as an adaptation to save the head from violent mechanical disturbance and to stabilize the gaze in a variety of behavioral situations.

Genitalia

Adult males use their abdominal appendages to capture and hold the female in tandem position during copulation. The cerci form a pair of superior (upper) appendages, but while in Zygoptera the paraprocts form a pair of inferior (lower) appendages, the epiproct forms a single one in Anisoptera (Figures 35.5(b) and 35.10(a,b)). Both are richly equipped with trichoid sensilla, which are presumably responsible for exact positioning of them at corresponding sites of the female prothorax. The female prothorax also contains specific sensory fields (Figure 35.10(c) and (d)), which may serve to ascertain that the mate belongs to the correct species.

The external female genitalia normally consist of three pairs of processes (main valves with short jointed styli, anterior or lower valves, and posterior or upper valves) forming together a typical endophytic ovipositor (Figure 35.10(e)). The upper and lower valves are sword-shaped, slightly curved structures possessing numerous denticles for interlocking with the substrate (Figure 35.10 (f)) and various sensilla for testing the substrate quality (Figure 35.10(e) and (g)).

The internal female genitalia allow for storage of sperm until oviposition, when the eggs are fertilized (Figure 35.11(d)). Sperm is inserted by the male from the secondary genitalia (Figure 35.5(f)). This is a complex organ, with different parts having remarkably different functions in each of the three suborders for attachment to the female and sperm storage, transfer, and removal (Figure 35.11(a)–(c)). For example, in Anisoptera the vesicle in which sperm is stored before insemination is modified into a segmented penis, while in the two other suborders the vesicle discharges onto a functional penis formed by a slide-like ligula (Zygoptera) or tube-like posterior hamules (Anisozygoptera).

Perception: The Sensory Organs and Neural System

The nervous system in Odonata is, as in most other insects, based on a double chain of ventral ganglia, one pair in each abdominal segment. The ganglia are fused in parts of the abdomen, mainly in the head region, where a large part of
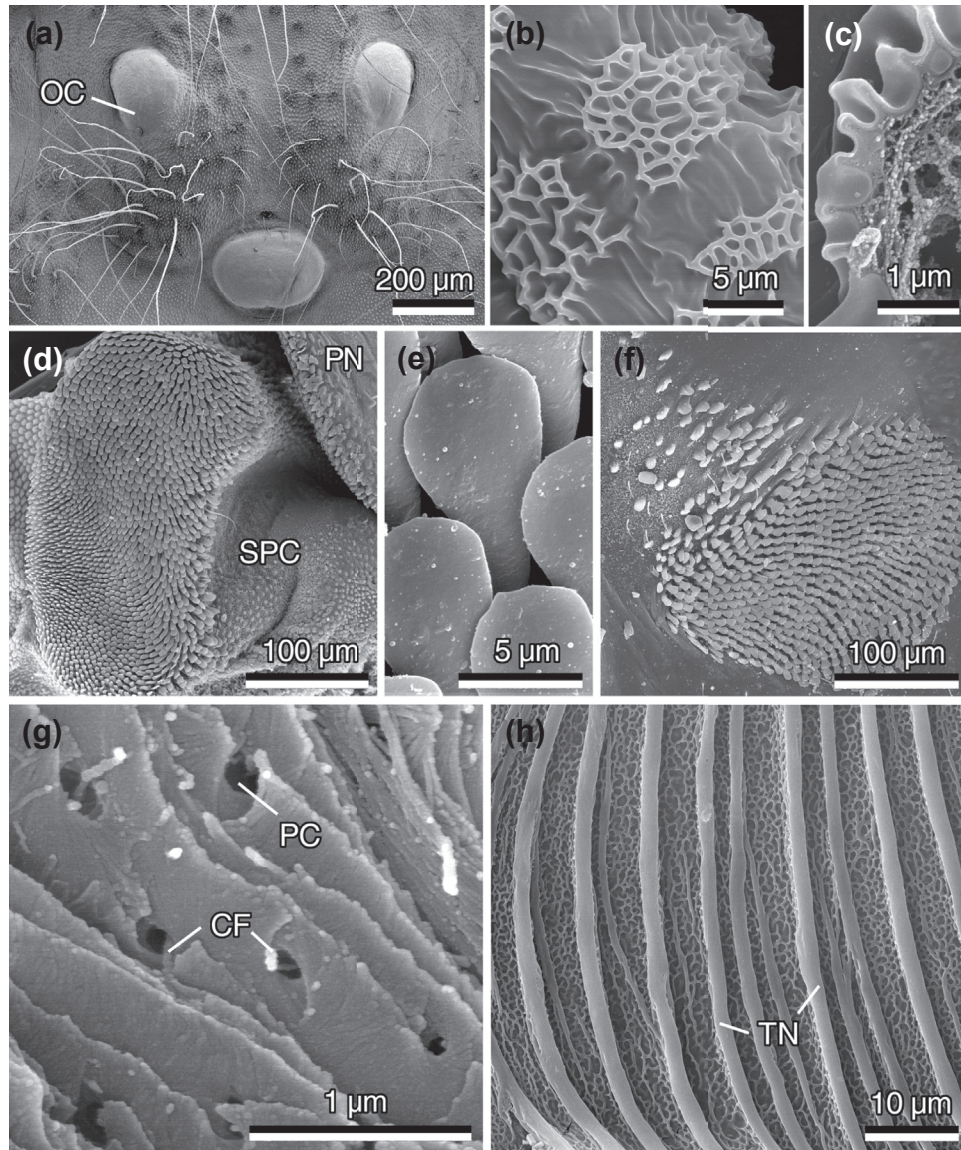
FIGURE 35.9 SEM images of odonate head and prothorax. (a) *Calopteryx splendens* head, frontal view; three ocelli (OC) and numerous trichoid sensilla are visible; (b, c) extensible neck membrane in *Ischnura elegans*, from the perspective of the surface (b) and (c) a section through the membrane; (d–f) head arrester system in *Lestes barbarus* (Fabricius, 1798), showing (d) the left postcervical sclerite (SPC) covered by (e) numerous cuticle protuberances near the prothorax (PT), with (f) corresponding microtrichia field on the rear surface of the head; (g) oblique fracture of the cuticle in *L. barbarus*; numerous porous canals (PC) with canal filaments (CF) are visible; and (h) fractured trachea reinforced with taenidia (TN) in the prothoracic region of *Erythromma lindenii* Selys, 1840. *Photos by SG.*

the "brain" is attributed to sensory neurons from the ommatidia, especially in adults (Tillyard, 1917).

Compound Eyes and Ocelli

The three ocelli (Figure 35.9(a)), present in all species, can distinguish light from dark, while the compound eyes provide sharp vision as well as color vision (including the UV spectrum) in many larvae and most adults (Corbet, 1999, pp. 89, 341). Eyesight is extremely well developed compared to other insect groups. Both larvae and adults have compound eyes. The number of ommatidia is small in the newly hatched larva, but new ones are added at the anterior part of the eye at each molt (Sherk, 1977, 1978a). The adult eyes are significantly larger than the larval ones, especially so in Anisoptera where large Aeshnidae can have more than 28,000 ommatidia per eye (Corbet, 1999). Many species increase the resolution of the eyes at the expense of binocular vision. Thus, the highest resolution in an adult dragonfly eye is straight ahead and in bands along the horizon. Some species also have vertical bands of high resolution that help them to capture prey from below (Sherk, 1978b). In some
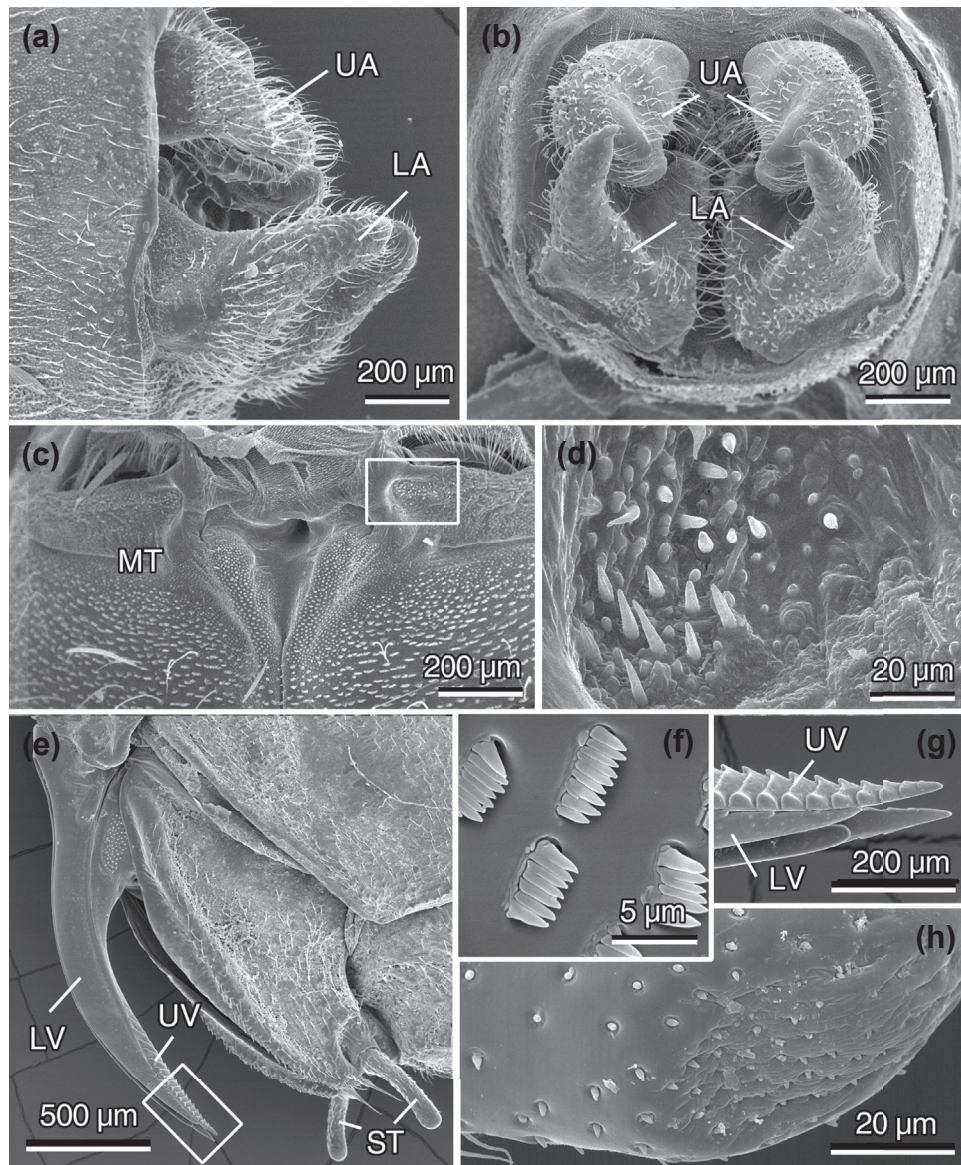
FIGURE 35.10 Details of some genital structure in dragonflies (SEM images). (a, b) Male upper (UA) and lower (LA) anal appendages in lateral view (a) of *Enallagma ambiguum* Navas, 1936, and posterior aspect (b) of *E. risi* Schmidt, 1961; (c, d) dorsal view of the mesothorax of the *E. ambiguum* female; this region is the attachment site for the male anal appendages and is richly equipped with trichoid sensilla; the white rectangle region (c) is also shown (d) enlarged; and (e–h) female abdominal structures in *Calopteryx splendens* showing typical endophytic ovipositor (e) with upper (UV) and lower valves (LV) and stylus (ST) in lateral aspect; the white rectangle region in (e) is also shown enlarged (g); (f) inner surface of the lower valvula covered with comb-like arrays of distally oriented microtrichia used for egg transport into plant tissues; the tip of the stylus (h) is richly equipped with numerous sensilla. *Photos by SG.*

species, e.g., *Aeshna cyanea* (Müller, 1764), *S. sanguineum*, and *I. elegans*, the dorsal rim of the compound eyes has specialized ommatidia believed to make polarized vision possible (Meyer and Lebhart, 1993).

Tactile Sensory Organs

While the antennae in adults are small and do not act as a major sensory organ due to the dominance of vision, the antennae in larvae are very important as tactile receptors.

The setae on the antennae are tactile setae, being long, bristle-like structures that generate a nerve impulse when moved in any direction. Tactile setae are also present on the feet and mouthparts of the larvae. These mechanoreceptors register movement and are essential both to prey detection and to avoid being preyed upon. The longer these setae are, the smaller movements of water (or air) they can detect (Corbet, 1999, p. 340). In adults, tactile setae are used, for example, to register speed when flying. The stylus at the ovipositor is also a sensory organ richly equipped with
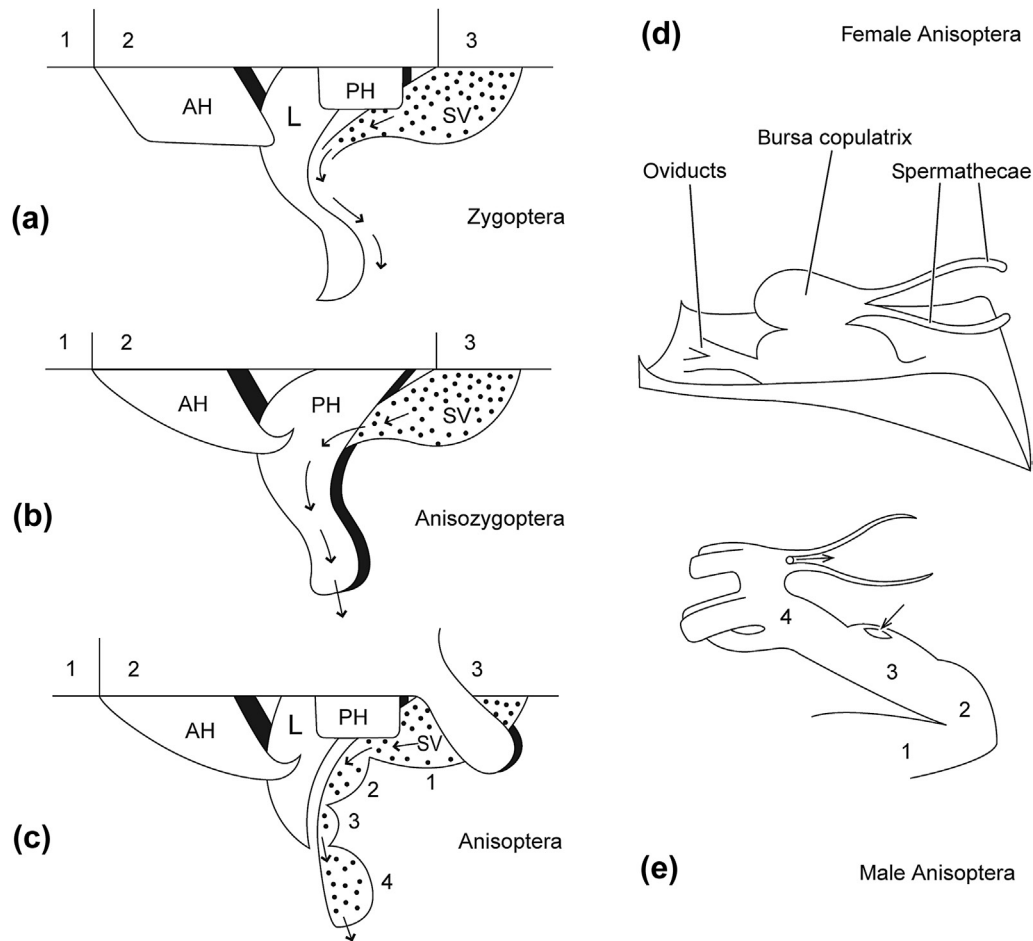
FIGURE 35.11   Schematic representation of odonate genitalia. (a–c) Male secondary genitalia of (a) Zygoptera, (b) Anisozygoptera, and (c) Anisoptera. Structures of the secondary genitalia are the anterior and posterior hamules (AH, PH), ligula (L), and sperm vesicle (SV). Paired structures are shown with black shadow. AH may be modified to hooks that can grip the female genital opening (b–c). Digits indicate abdominal and sperm vesicle segments and arrows the route of sperm on insemination. The female genitalia of Anisoptera are depicted in (d) and in (e) the male sperm vesicle; note how the vesicle fits into the spermatheca. Arrows indicate the entrance and exit point for sperm on the vesicle. *Original drawing by KD.*

sensilla to insert the egg correctly into the substrate during oviposition (Figure 35.10(e) and (h)). Other sensillae are used in thermoregulation, reacting to unsuitable temperatures, or as chemoreceptors when feeding. Odonates also seem to have an olfactory sense; this is suggested by the presence of certain receptors described on the antennal flagellum of adult *Libellula depressa* Linnaeus, 1758, which seem to react to chemical stimuli (Rebora et al., 2012).

Respiration

Larval Gill Systems

Dragonfly larvae possess one or more organs that have a respiratory function. All Anisoptera have internal rectal gills, the branchial basket. The gills consist of richly tracheated expansions of the rectal pads. The shape of the rectal gills varies between and sometimes even within Anisoptera families

(Tillyard, 1917), but the functions of the different shapes remain unknown. The gills are constantly supplied with fresh, oxygen-rich water via a pumping movement of the abdominal muscles. The pumping function can also be used for jet propulsion to speed up swimming. In gomphid larvae that burrow deeply in sediments, the elongate, tubular terminal abdominal segment serves as a breathing tube reaching the water above the sediment (cf. Microhabitat Occupancy by Larvae).

Although no recognizable gills have been formed in the rectum of Zygoptera larvae (Corbet, 1999, p. 76), they still ventilate the rectum most of the time by making pumping movements, which is interpreted as gas exchange. However, it seems that the caudal appendages (caudal lamellae) are the major sites of gas exchange (Miller, 1995). The caudal appendages are formed by the paraprocts and, except for the Chlorocyphidae, by the epiproct. The shape is quite variable (Figure 35.12(a) and (c)–(g)), from elongate to broad and bag shaped (saccoid, Figure 35.12(b)) as in
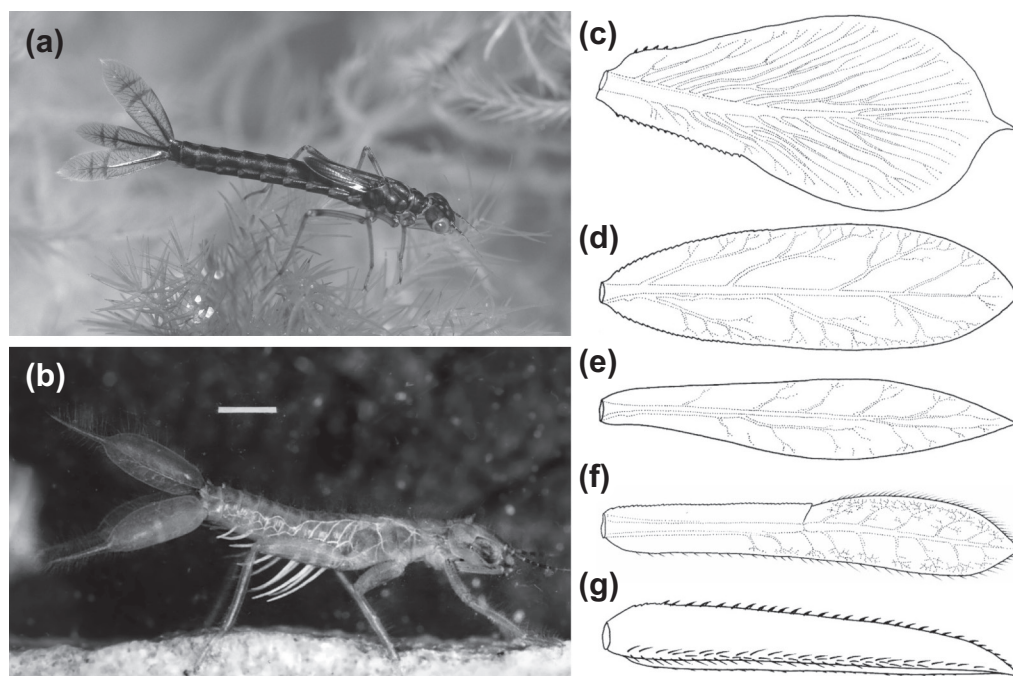
FIGURE 35.12   External structures of the respiratory systems of Zygoptera larvae. (a) Larva of a Coenagrionidae, *Enallagma cyathigerum*, with three caudal lamellate appendages in lateral view. *Photo Karsten Grabow*; (b) larva of an Euphaeidae, *Epallage fatime*, with three saccoid appendages in lateral view. *Photo Ulf Norling*; (c–f) various shapes of single appendages of Coenagrionidae in lateral view, including (c) broadened (e.g., *Ceriagrion*), (d) normal lamellate (*Africallagma* Kennedy, 1920), (e) lanceolate (*Agriocnemis* Selys, 1877), and (f) with a nodus (*Pseudagrion* Selys, 1876); and (g) triquetal appendage of *Platycypha* Fraser, 1949 (Chlorocyphidae). *Drawings by Ole Müller.*

Euphaeidae. All types of caudal appendages are suffused by tracheae, through which gas is transported, but their role in respiration is surely different. Lamellae-shaped appendages with great surface area-to-volume ratio presumably play a greater role in gas exchange than those with a smaller ratio. Species with appendages of the latter type usually live in well-oxygenated habitats (Corbet, 1999, p. 76ff.).

Two other types of gills occur in Zygoptera. In the former "Amphipterygidae" (see above) and in Pseudolestidae, the larvae bear two tufts of tracheal gills, one on each side of the anus. Although all species have caudal appendages, the gill tufts seem to play the main role in gas exchange (Corbet, 1999, pp. 77–78). Finally, the Polythoridae and Euphaeidae, for instance *Epallage fatime* (Charpentier, 1840), (Figure 35.12(b)), possess lateral abdominal gills in the form of unsegmented filaments at segments 2–7 and 2–8, respectively.

Oxygen Demands

Larvae often survive relatively low values of dissolved oxygen. Lethal oxygen concentrations (LC_{50}-values) were between 4% and 26% in lentic water species (at 20–30 °C). The burrowing larvae of the lotic water species *Onychogomphus forcipatus* (Linnaeus, 1758), had LC_{50} values of ~15% at 25 °C (Jacob et al., 1984). In Anisoptera the pumping frequency is increased with decreasing levels of dissolved oxygen—that is, more water is transported to the gills. If the conditions become hypoxic, Anisoptera stick their anal pyramid over the water surface and breathe atmospheric oxygen. In contrast, Zygoptera larvae may place themselves near the water surface where oxygen content is often higher due to diffusion.

Tracheal System of the Imago

As in all insects, adult odonates breathe by means of tracheae, which are of ectodermal origin. Air is drawn into the tracheal system via spiracles (Tillyard, 1917). The great flight muscles are supplied through a modified tracheal system. During wingbeats the vertical and sideways movements of the thoracic plates cause volume changes of the thorax, which drive air into and out of the tracheae (Miller, 1995).

Physical-Gill Respiration

Adult dragonflies are usually recognized as aerial/terrestrial organisms. Many Zygoptera (e.g., Calopterygidae and Coeangrionidae), however, oviposit under water; and in some cases, the male accompanies the female in tandem. The imagines can go as deep underwater as 1 m, and the duration of uninterrupted underwater oviposition is often 30 min. In *Enallagma cyathigerum* (Charpentier, 1840), even 185 min of uninterrupted oviposition with both female

and male submerged has been observed (S. Schulz unpublished Diploma thesis). The underwater respiration depends on the physical-gill action of the air bubble investing the entire insect (body and wings). The wings stay perfectly dry as observed in *Calopteryx haemorrhoidalis* (Van der Linden, 1825), which could directly fly off after passing through the water surface. Water currents and movements of the insect are essential to the function of the physical-gill, since they become asphyxiated after about 10 min (Corbet, 1999, p. 31).

Thermoregulation

To maintain activity the adult odonate must keep its body temperature within a particular range and largely independent of the ambient temperature. Species that spend most of their active period on perches and make only short flights (perchers), thermoregulate primarily by postural adjustments to sunlight. A striking example is the obelisk posture where the abdomen points vertically toward the sun, and the body's shadow is reduced by 50%, thus reducing sunray exposure. At cold ambient temperatures, the insect may bask at a warm or reflective substrate to receive warmth from the surface. Some of the species that fly continuously (fliers) are endothermic regulators during flight. They control the body temperature through adjustment of the metabolic heat production (by alternately using gliding or powered flight)

or by controlling the heat loss by altering haemolymph circulation between thorax and abdomen (May, 1976). At cool ambient temperatures muscle vibration provides heat for takeoff. Besides these methods, reversible color change as well as adaptive activity patterns and microhabitat selection have been identified as thermoregulation strategies (Corbet, 1999, p. 282ff.).

Flight

The flight apparatus of adult Odonata is primitive in terms of the arrangement of muscles and cuticular plates of the thorax. They differ from all other insects in that the great muscles of the synthorax are directly connected with the wing bases (Tillyard, 1917). This enables relatively independent control of each wing, which may be one of the key factors behind the versatility of dragonfly flight (Miller, 1995). Odonates are capable of great acceleration, the maximum flight speed being 10–15 m/s, and they can execute rapid maneuvers in a very limited space. Patterns of wing movement during flight differ between Anisoptera and Zygoptera depending on their different morphological features (Figure 35.13; Rüppell, 1989). In most Zygoptera and *Epiophlebia*, the fore and hind wings always move in opposite directions. In Anisoptera, such counter stroking occurs in special maneuvers such as flying on the spot. Their main wing beat pattern, however, involves phase shifting of the fore
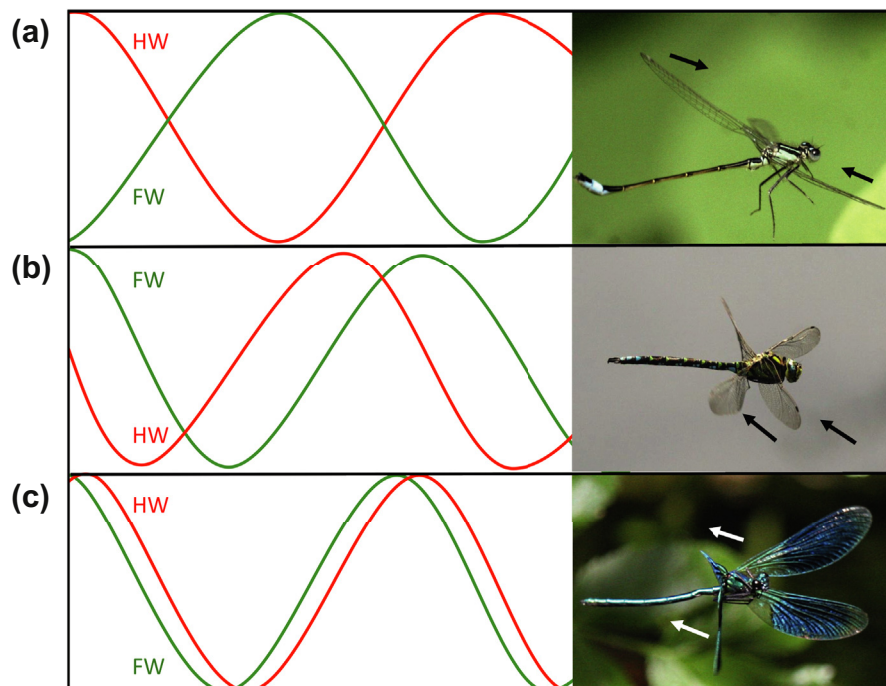

FIGURE 35.13 Different phase relationships between forewings (FW, green line) and hindwings (HW, red lines): (a) normal flight in Zygoptera: counterstroke movement where fore- and hindwings beat alternately (the example shows *Ischnura elegans*); (b) normal flight in Anisoptera: phased movement with hindwings leading (*Aeshna cyanea*); and (c) synchronized movement: all wings beat in the same direction at the same time used by Calopterygidae, except courting flights, and by Anisoptera in short bursts (*Calopteryx splendens*). *Figure and photos by Georg Rüppell and Dagmar Hilfert-Rüppell.*

and hind wings, where the two pairs of wings follow each other with a delay of about one-fourth period. This mode increases the power output. All Odonata may beat both pairs of wings nearly simultaneously in the same direction for a few wing beats in maneuvers such as backward or upward flight. Males of *Calopteryx* spp. use parallel wing beating most of the time when displaying their colored wings to rivals. The benefit is a greater net force, usable for acceleration; the cost is greater power expenditure. Due to their high wing surface-to-body weight ratio, many species, such as those in the families Aeshnidae and Libellulidae, have the ability to glide, i.e., to fly longer distances without active wing beats—a phenomenon that is generally rare in insects.

Reproduction

Sexual reproduction is obligatory in Odonata. So far, parthenogenesis has only been detected in nature in the geographically isolated population of the American *Ischnura hastata* (Say, 1839), on the Azores Islands (Cordero Rivera et al., 2005).

Sexual Dimorphism

Over three-fourths of odonate species are sexually dimorphic as adults, i.e., the female has a different and in many cases more cryptic coloration than males. In males, colors are more clear and vivid than in females; and in many species, a blue/white waxy pruinescence is developed on the abdomen and sometimes also thorax with sexual maturation (see ultrastructures in Figure 35.8). Teneral males of such species resemble females in color. The same type of pruinescence is sometimes found in old females. Pruinescence is widespread in Libellulidae but is also present in other families, e.g., Lestidae (Corbet, 1999, p. 281). In some species females have more than one color morph. Gynochrome females have the normal female coloration (often green/yellow on dark background, e.g., in species of *Ischnura*), while androchrome females resemble males in color (blue on dark background). The assumed function of these differences in color is to limit excess male harassment, which is believed to otherwise have a negative impact on female fitness. However, the purpose of female color polymorphism is under ongoing debate.

Mating Systems

Odonates have several mating systems and are thus ideal organisms for studies of sexual evolution. Many species employ scramble competition; females arrive "unpredictably" to the water, and the male who responds most promptly is most successful in mating (Fincke, 1982). In many other species, males defend territories along the water, sometimes but not always at the best oviposition sites. Males compete with each other for territories, and most individuals can only keep a territory for a limited

time window (hours to days). Territorial conflicts do not always include physical fighting; for instance, display flights can be an alternative in species with colored wings as most Calopterygidae (Corbet, 1999, p. 463ff.). Males often perch on a conspicuous location within his territory, from where he can observe the arrival of females as well as competitors. Males of some species perform patrol flights, sometimes along water courses, enabling several males to coexist within a limited area; territorial disputes arise when males meet each other (Corbet, 1999, pp. 438–441). Alternative mating tactics are found in some other species. Several males can coexist in the same territory if a dominance hierarchy is present, as in *Libellula luctuosa* Burmeister, 1839. Satellite/sneaker males are found in many species, for example, in *Calopteryx maculata* (Palisot de Beauvois, 1807), and *Nannophya pygmaea* Rambur, 1842, where matings can occur inside or outside the territory of the defending male when he is occupied elsewhere (Corbet, 1999, pp. 458–460).

The Mating Process

During mating, the male grasps the female with his anal appendages. In Zygoptera, the male appendages grasp the prothorax; while in Anisoptera, the head of the female is grasped. After forming this precopulatory tandem, the male transfers sperm from the genital opening ventrally on S9 to the secondary genitalia on S2 (Figure 35.11(a)–(c)). The female lifts her abdomen to lock the valves of her ovipositor or genital plate to the secondary genitalia of the male, and copulation begins. The male first uses his penis (or lobes/barbs on its surface) to remove most of any previous sperm stored in the female bursa copulatrix before inserting his own sperm (Figure 35.11). Sperm removal as a key mechanism of sexual evolution has been extensively studied (Waage, 1979; Corbet, 1999, p. 502ff.). Copulation lasts from only a few seconds in some species (e.g., *Libellula quadrimaculata* Linnaeus, 1758) up to many hours in *Ischnura senegalensis* (Rambur, 1842) (Corbet, 1999, pp. 523–525). The copulatory position of odonates, known as the mating wheel (Figure 35.14), is unique in that the couple can fly in copula.

Oviposition

As males are able to remove most of the sperm from previous matings, there is an evolutionary pressure for the male to remain attached to, or in the vicinity of, the female until she has deposited her eggs. In some species, the male remains attached to the female, flying with her to the egg laying locality in synchronized flight (tandem flight, Figure 35.15(a)). The male guides the female, and she deposits her eggs. This is called tandem guarding. In other species, the male detaches from the female but hovers close to her in an effort to prevent other males from mating with her
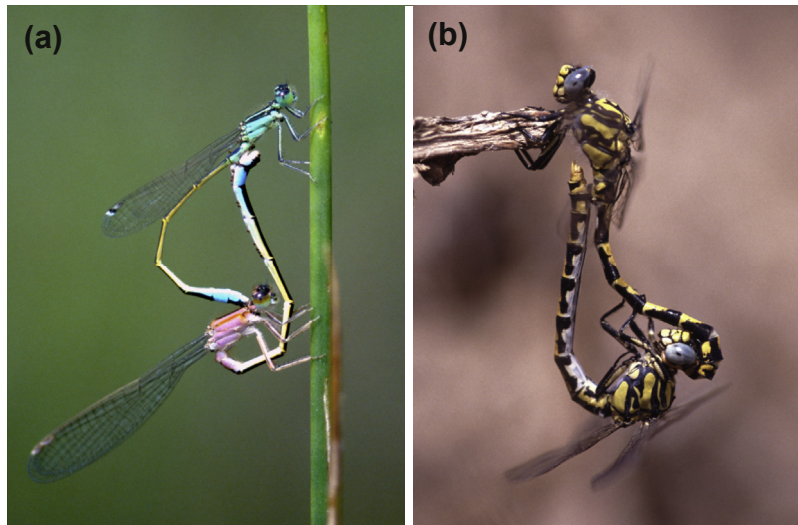
FIGURE 35.14 Copulatory wheel of: (a) a zygopteran, *Ischnura elegans*; and (b) an anisopteran, *Onychogomphus uncatus*. Note that the appendages grasp at the prothorax in Zygoptera, but over the head in Anisoptera. *Photos by FS.*
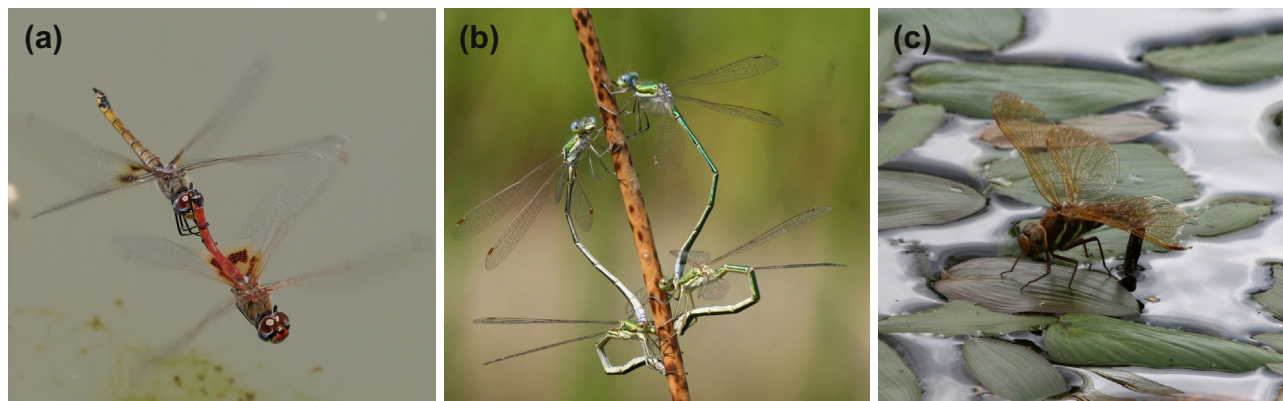

FIGURE 35.15 Oviposition behavior of Odonata. (a) Contact guarded (tandem) exophytic oviposition by *Tramea basilaris* (Palisot de Beauvois, 1817); (b) contact guarded endophytic oviposition by *Lestes virens* (Charpentier, 1825), note the marks of previously deposited eggs in the stem; and (c) unguarded endophytic oviposition by *Aeshna grandis* (Linnaeus, 1758). *Photos (a) Ida Suhling, the others FS.*

(noncontact guarding). In other species again, the female lays eggs unguarded (Conrad and Pritchard, 1992).

All Odonata have panoistic ovaries with numerous separate oocyte strings (ovarioles), longitudinally ordered in the abdomen. Most odonates are assumed to have continuous oocyte production during their entire mature life span, and short egg-laying periods interspersed with resting (Corbet, 1999, p. 21ff.). Karlsson et al. (2010) divided species of Libellulidae into those with continuous versus stepwise egg production. Continuous egg production enables the females to lay eggs all the time, thereby facilitating risk spreading; however, this also increases the time spent at oviposition sites and thus the predation risk. In the opposite strategy, maturing the eggs stepwise permits rapid deposition of a large clutch on a single occasion, thereby reducing predation but with no risk spreading.

The ovipositor of Zygoptera and Aeshnidae has evolved to facilitate oviposition into substrates such as plants. A pair of cutting valves, covered by outer valves when at rest, makes a hole in the plant tissue by alternating movements, and the eggs are inserted by muscles contracting in S9 (Matushkina and Lambret, 2011). In other Anisoptera there is a gradual reduction of ovipositor complexity, ending with a simple genital plate in Corduliidae and Libellulidae. The eggs emerge under the plate and accumulate under S9, until they are deposited (e.g., when the female dips her abdomen into water).

Oviposition can take place while the female is flying (Figure 35.15(a)) or when the female is settled on the substrate such as plants, mud, sand, or rock (Figure 35.15(b)–(d)). A female can oviposit many consecutive times in her reproductive life. Species with endophytic egg laying in general deposit fewer than ~300 eggs at one oviposition event, while many exophytic species lay 1500 or more eggs in each clutch (Corbet, 1999, pp. 36–41).
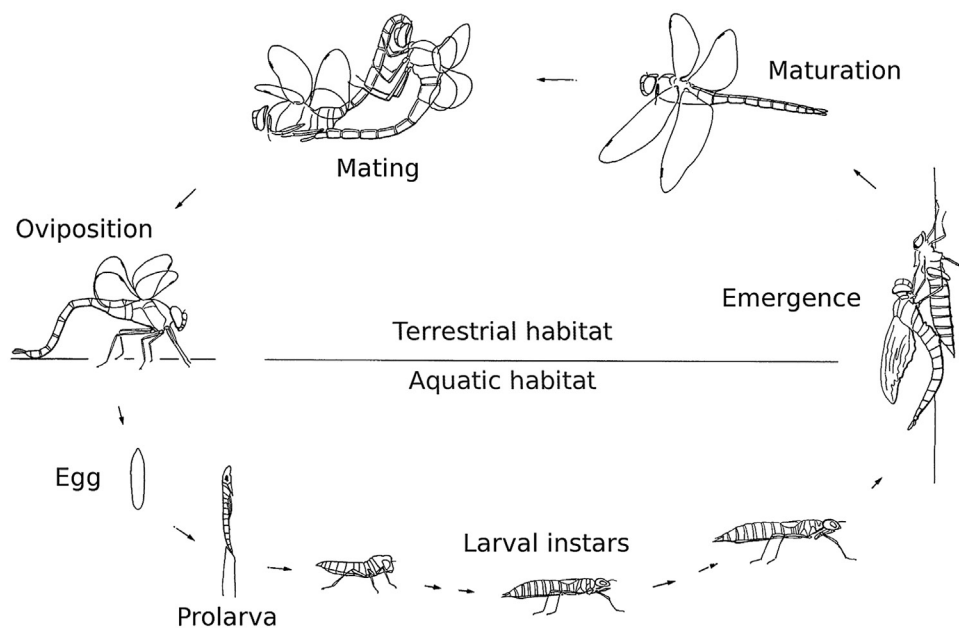
FIGURE 35.16   Life cycle of Odonata. The depicted life cycle stages are the same in all Odonata, but the prolarva may be extensively reduced. The time spent in each of the stages varies strongly between families and between species within families. *Original by Hansruedi Wildermuth.*

Life Cycle

Odonata are hemimetabolous insects, i.e., they do not have a pupa stadium. They possess a semiaquatic life cycle, with an aquatic larval stage (a few larvae are terrestrial) and a terrestrial, volant adult stage (Figure 35.16). The egg development is mostly aquatic but may also occur in or on wet soil or in plant tissue. Otherwise, the impression is that of an overwhelming variability. The number of larval instars varies from 8 to 17 between species and from 12 to 17 within one species (even between siblings) (Sternberg, 1995). Voltinism ranges from four (maybe more) generations per year to about one generation in three to maybe even 10 years. Also within a given species, there are rarely any fixed development times. Species of *Lestes* Leach, 1815, do, however, generally seem to be univoltine. In other species, there is variation between the populations from different latitudes. An example is *I. elegans* varying from having at least two generations per year in the Mediterranean to one generation in 2 years in parts of Britain (Corbet et al., 2006).

Egg Development

Eggs may have either direct or delayed development, where a period of diapause is needed. In some species both may occur. In eggs with direct development, hatching occurs within 1–8 weeks, temperature being the most important regulating factor (Corbet, 1999, p. 52). Such eggs have a continuous embryonic development, while development in diapause eggs is halted at a stage in which it overwinters. Egg diapause either takes place when the embryo turns around in the egg at an early developmental stage or when the embryo is fully formed (with clearly visible eyes through the eggshell)

(Ando, 1962). Diapause eggs are common in temperate species (many *Aeshna* Fabricius, 1775, *Lestes*, *Somatochlora* Selys, 1871, and *Sympetrum* Newman, 1833) but are uncommon in tropical species where fewer cases are reported, probably all of the latter type. One instance is *Pseudostigma accedens* (Selys, 1860) (Corbet, 1999, p. 56). During the period before diapause and even during diapause, embryonic development can proceed at very low temperatures, e.g., at 0 °C in *Lestes congener* Hagen, 1861 (Corbet, 1999, p. 59).

Odonata have kept the metabolic temperature reaction norm of their presumably tropical origin, i.e., being warm adapted, even if they occur in the boreal zone (Pritchard et al., 1996). Thus, egg hatching is temperature dependent and, especially for diapause eggs, very synchronized in spring when the appropriate water temperature is reached. In some species, a small part of the eggs delay their hatching until a higher water temperature is reached, thus spreading their risk in an unpredictable environment (Sternberg, 1995). For an embryo developing in an egg above the waterline (many species deposit their eggs in plant stems that may dry out during winter or on moist ground with no free water), desiccation is a problem but is prevented to some extent by thicker eggshells. Predators, such as water mites and fish as well as parasitoid wasps otherwise eat many eggs before they hatch. Fungal and bacterial infections may also be a problem, but there seem to be certain antibiotic functions in the exochorionic jelly of some species.

Larval Development

When hatching from the egg, the first molt usually occurs directly after or even during this process, so that only the
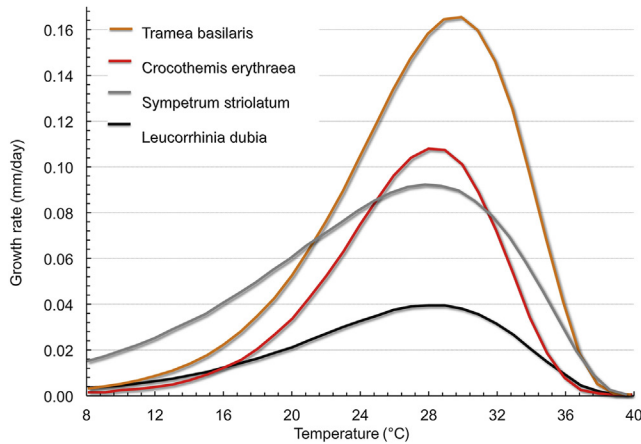
FIGURE 35.17 Temperature response of four Libellulidae with different distributional ranges. The mainly boreal *Leucorrhinia dubia* (Vander Linden, 1825), the temperate *Sympetrum striolatum* (Charpentier, 1840), the tropical-temperate *Crocothemis erythraea* (Brullé, 1832), and the tropical *Tramea basilaris*. The figure is simplified by only showing fitted response curves *(by O'Neill functions.)* for growth rates; measurements were taken at five constant temperatures of 16, 20, 24, 28, and 32 °C. *Original FS.*

second larval instar is freely visible. The first instar is functional only in some species that oviposit away from the water; it forms a prolarva that is able to reach the water by jumping, as in *Chalcolestes viridis* (Vander Linden, 1825). Conventionally, the instars or stadia are typified by counting backward, i.e., the ultimate instar is F or F−0 (read: final minus zero), the penultimate (F−1), and so on. The growth ratio (i.e., size increase from instar to instar) varies relatively little and falls between 1.2 and 1.4 when using head width as size measure (Corbet, 2002).

The duration of the larval development may vary among species by a factor of at least 50 (<30 days to several years), and by a factor of 10 within a species, as in *I. elegans* mentioned above. Larval growth occurs at species-specific rates that are governed by exogenous (environmental) and endogenous factors. The major exogenous factors are food supply and ambient temperature (Krishnaraj and Pritchard, 1995). First, the amount of food available and the type of prey directly translates into growth rate, with high amounts and quality of food allowing rapid growth. Ingestion rates seem to vary (Stoks et al., 2005) as well as the functional response and the prey handling time (see below)—all factors that would lead to variations in growth rate. Second, an increasing ambient temperature accelerates the rate of growth up to a species-specific optimum as shown in Figure 35.17. The optimum for growth ranges between 20 °C and more than 30 °C; but less than 20 species have been sufficiently investigated. At least in Libellulidae, the optimum seems to be generally high, even in boreal species. The maximum growth rates do, however, vary significantly as well as the factor of growth rate increase with increasing temperature (the slope of the response function). In the example

(Figure 35.17) both values were higher in the tropical species, i.e., they are more specialized to higher temperatures. The lower minimum for larval development in Odonata is not yet well studied, but it seems to be between 8 and 12 °C.

The major endogenous factor governing larval growth is diapause—interrupting development during unfavorable environmental conditions. Most species in the temperate zone stop development during winter, which is achieved by photoperiodic reactions (Norling, 1984; Corbet, 1999, p. 228ff.). Typically, short photoperiods induce a diapause that commits the larvae to hibernation, which may occur in various instars and in any year of the larval life. The critical day length for this induction depends on the latitude. At about 40° N, it may be as short as 10 h, and increase to 15 h at 58° N and to even 19 h at the Arctic Circle (Norling, 1984; Flenner et al., 2010). In addition, a second mechanism may occur preceding the year of emergence—the long photoperiods characteristic of summertime may induce a diapause mainly in later instars, thus delaying their development. This may lead to an accumulation of F−1 larvae during summer, followed by their rapid entry into the final instar close to the autumn equinox, as shown for *Leucorrhinia dubia* (Norling, 1984). The various photoperiod controls eliminate any possibility that metamorphosis or emergence might occur before the advent of winter. It has not yet been determined whether a similar process also occurs in tropical dragonflies to achieve seasonal regulation (see below).

Metamorphosis and Emergence

Metamorphosis consists of irreversible changes in morphology, physiology, and behavior that take place between the final larval instar and emergence, the latter being the molt that produces the adult dragonfly. Metamorphosis begins several days before emergence and is under endocrine control, being induced by an increase in ecdysone. Among the first external signs is the orientation and swelling of the wing sheets and a change in the pigmented area of the compound eyes. As one of the last developmental steps, the breathing organs must be adapted to breathing air instead of water. The labium also has to be transformed into its adult shape. The larvae are unable to catch prey during the transformation, which may last several days. After these transformations, the larva has to leave the water within a short time. When leaving the water the larva attaches itself to a support with its legs. Two types of posture at emergence are distinguished. In type 1 (Figure 35.18(a)) the larva sits in a horizontal to vertical position (90°), which allows emergence at shorelines without vegetation and characterizes most Zygoptera and Gomphidae. All other Anisoptera perform emergence of type 2 (Figure 35.19(b)), where the larva needs an overhanging support to remove the larval skin (exuvia).

Molting the last larval skin and preparing for aerial life may take from about 20 min up to several hours, depending
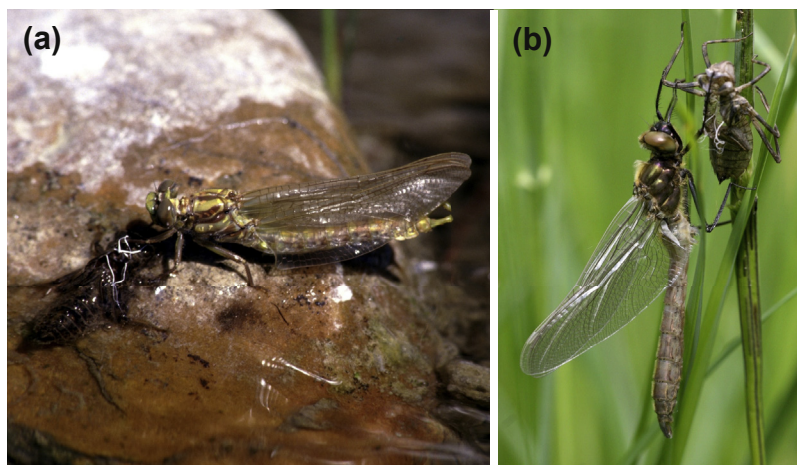
FIGURE 35.18   Freshly emerged Odonata sitting on the respective exuviae. Left: type 1 emergence of the gomphid *Onychogomphus uncatus*; right: type 2 emergence of the corduliid *Cordulia aenea* (Linnaeus, 1758). *Photos FS.*

on the species. This is a particularly risky phase because the dragonfly cannot escape predators. In addition, mechanical damage, for instance during periods of strong wind, may cause high mortality due to incomplete ecdysis. Larval mortality at emergence is in the range 5–28% (Jakob and Suhling, 1999). The exuvia left behind is robust and may remain at the support where the emergence occurred for weeks, particularly if the sites are protected from rain.

Seasonal Patterns

The option of collecting exuviae offers a powerful method of quantifying population density, sex ratio, and seasonal regulation. By undertaking this extensively, P.S. Corbet (see review in Corbet, 1999) found a dichotomy of temperate-centered species that is demonstrated by cumulative emergence curves (Figure 35.19(a)). One group overwinters in the final instar and has a highly synchronized emergence; in the temperate zone, this usually occurs in spring ("spring species"). The other group ("summer species") overwinters in one or several earlier instars, and has, therefore, a less synchronized emergence. These patterns are not fixed within a species. When two populations of *Onychogomphus uncatus* (Charpentier, 1840), at adjacent habitats that varied in water temperature were compared, one of them was found to belong to the spring type and the other to the summer type (Suhling, 1995). *Gomphus vulgatissimus* (Linnaeus, 1758), demonstrated high variation in emergence pattern between years as well as between sites in Germany (Figure 35.19(b)). Onset as well as duration of emergence was affected by the ambient temperature differences between the habitats (small stream vs large river), as well as between the annual differences in the temperature before emergence. The data from the river may reflect a higher amount of cohort splitting (i.e., one part of a cohort is emerging 1 year earlier or later than the main cohort). At higher latitudes, with decreasing length

of the summer season, the emergence patterns become more similar.

In the tropics, the major seasonal difference is that between the dry and the rainy season, which is distinct in arid regions but less so in more humid regions. Taking this into account, some variation in flight season may be expected along gradients from wetter to more arid conditions. In fact, *Ictinogomphus ferox* (Rambur, 1842), emerges throughout the year in Uganda (Miller, 1964) and most of the year along the Okavango River but has a shorter flight season in arid central Namibia, namely from October to April (Suhling and Martens, 2007). Nonetheless, many species in the tropics have well-defined seasonal phenology patterns, but the mechanisms for time regulation are not yet understood.

Prereproductive Period

The newly emerged adult normally leaves the water by way of a so-called maiden flight. In the first hours after emergence, the cuticula of the dragonfly is still soft and its flight insecure. However, this has to change rapidly because a dragonfly may lose much of its weight in the last phase of its larval life due to the labium transformation. In order to become sexually mature, it has to compensate for this by hunting (mainly flying) insects. In females, weight has to be increased in order to produce eggs. During maturation, which may take from a few days to a few weeks, a dragonfly's colors—always pale at emergence—intensify.

Adult Life Span

In the temperate climate zone, mature adults usually live for up to 2 months, but studies on *Coenagrion puella* (Linnaeus, 1758), in England revealed that the actual lifetime is often much shorter due to bad weather (Banks and Thompson, 1985). In species that commonly breed in temporary waters, the adults may enter an extended phase of diapause, which
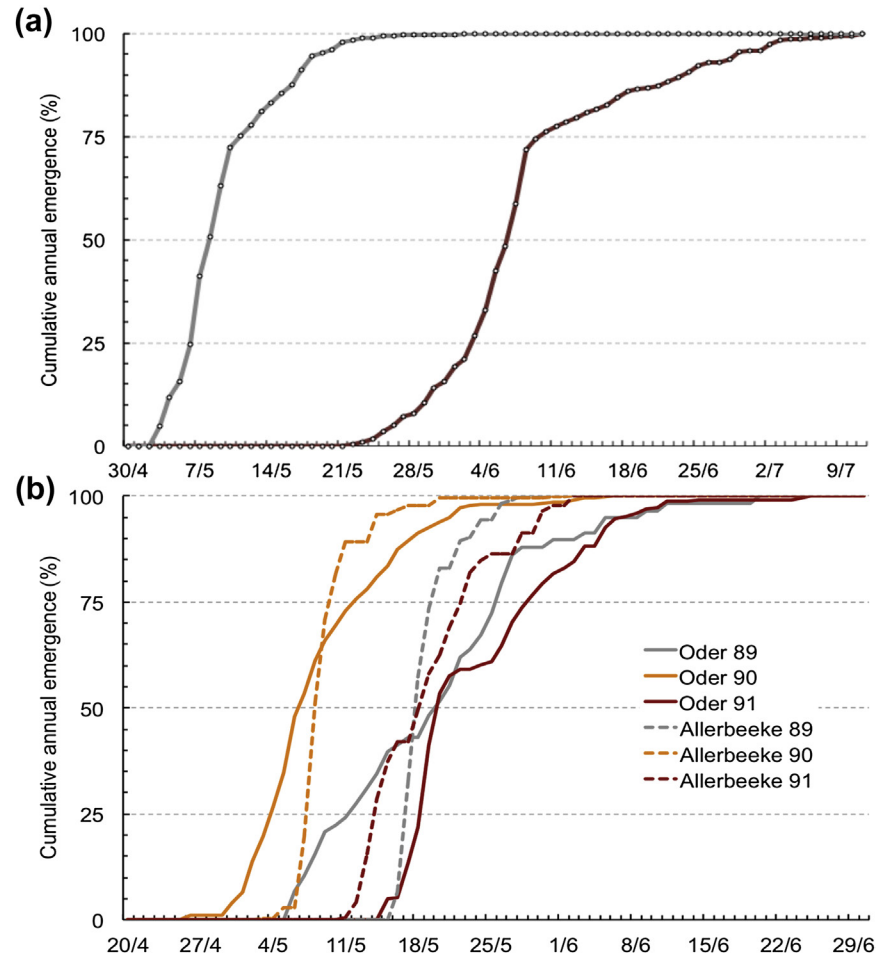
FIGURE 35.19   Annual emergence. (a) The differences in emergence between a spring species (gray line), *Gomphus vulgatissimus* and a summer species (red line), *Gomphus flavipes* (Charpentier, 1825); and (b) annual variability of emergence of *G. vulgatissimus* from a small stream (Allerbeeke) and a large river (Oder) in three consecutive years. *Drawn after data of Dietrich Kern and Ole Müller.*

they spend away from the water. In this phase, the gonads do not mature. Tropical species often seem to have greater longevity, up to several months longer in some cases. Thus, in the tropics and particularly in temporary water species, the adult stage may last longer than the larval stage, whereas the opposite is most common in the temperate zone. A study comparing data on 35 species indicated that senescence (age related mortality) is higher in males than in females in species that exhibit territoriality (Sherrat et al., 2011).

Life Cycle Types and Voltinism

The duration of a generation in dragonflies can range from one generation a year (univoltine) to up to four generations in a year (multivoltine), and even to only one generation in two (semivoltine) or three or more years (partivoltine). A true dichotomy between tropical and temperate life cycles, as proposed by Corbet (1999, p. 220), is not well supported by evidence. Instead, the analyses of Corbet et al. (2006) on latitudinal patterns of voltinism implied that there is a

gradient in life cycle duration. In the following paragraphs, we adapt the idea of Corbet (1999, Table 7.3) to categorize odonate life cycles.

Regulated Life Cycles

These life cycles are characterized by a diapause, i.e., endogenous regulation, in one or more than one life cycle stage. The diapause serves to cope with unsuitable environmental conditions, such as cold (hibernation, winter) or drought (aestivation/siccatation, dry season). The diapause may however be facultative, i.e., absent in populations living in more favorable environments.

> *Obligate Diapause in the Egg Stage*: Hatching from the egg occurs in spring or with onset of the rainy season, and larval development takes 2–4 months. The embryonic diapause may take place in various developmental stages. In the temperate zone, it occurs in late summer and winter. The life cycle is obligatory univoltine as in most species of *Lestes* and certain *Sympetrum* species.

Facultative Diapause as Prereproductive Adult: In these species, imagines aestivate during the dry season when habitats may dry out. Most species are univoltine. Examples are phytotelmata and tree-hole breeders in seasonal rainforests, e.g., *M. caerulatus*, as well as species occurring in savanna habitats (e.g., *Crocothemis divisa* Karsch, 1898), and species of summer dry subtropics. The variation between populations may be great in species of this type, depending on the environment in which they occur. A well-studied example is *Sympetrum striolatum*, which aestivates for 3–4 months as prereproductive adult in the Mediterranean. In central Europe, aestivation is facultative and shorter; and in northern Europe, it seems to be nonexistent. Also, the egg development may be direct or interrupted by a diapause.

Hibernating Adult: An obligate diapause in the prereproductive adult occurs in late summer and winter as in univoltine *Sympecma* Burmeister, 1839, species. Reproduction occurs in early spring and development lasts 3–4 months.

Facultative Diapause Mainly in the Larval Stage: This usually occurs in one or more later instars in winter, or in summer and winter. Occasionally there may also be an egg diapause in winter. The development is uni- to partivoltine and requires three or more years (sometimes up to 10 years at or above the Arctic Circle). This life cycle type is probably present in most temperate and boreal species but also in many lotic waters and high altitude species in the tropics.

Unregulated Life Cycles

These are characterized by lack of diapause in all life stages and by facultative multivoltinism. The development takes between 2–3 and 9 months (in the winter generation) and depends only on exogenous factors. Where these species live at high latitudes, they may be uni- or even semivoltine due to low temperatures. This type of life cycle exists in temperate as well as tropical odonates, but is presumably much more common in tropical species.

Life Cycles with Obligate Habitat Change within One Generation

The larvae usually develop very rapidly in perhaps 30–60 days in one water body, and the oviposition takes place in another water body after an episode of dispersal that may cover up to several thousand kilometers. There is no diapause in any life cycle stage; thus, development is unregulated. However, the onset of migration may involve some endogenous control. The life cycle is well suited to temporary waters; but breeding may take place also in other kinds of habitats. The species in this group, e.g., *Pantala flavescens* (Fabricius, 1798), are obligate migrants as described below (Dispersal and Migration).

GENERAL ECOLOGY AND BEHAVIOR

Foraging

Larval Foraging

Being obligate carnivorous predators, odonate larvae feed on all kinds of animals they can overcome, and the type of prey mainly depends on the habitat of the larva. Many Zygoptera and Libellulidae feed on plankton; Aeshnidae feed on larger prey including other odonates (Figure 35.20), small fish, and tadpoles. Burrowing species such as Gomphidae feed mainly on other bottom dwellers, such as Chironomidae larvae and Oligochaeta. There are distinct foraging modes: species may be active to sedentary and visual to tactile; these modes can occur separately or combined depending on species (Pritchard, 1965; Corbet, 1999, p. 88). An active larva searches for prey, climbing or even swimming as it does so. A sedentary larva stays motionless in a sit-and-wait mode until a suitable prey approaches. A visual larva is dependent on eyesight for identifying and capturing its prey, while a tactile

FIGURE 35.20   A larva of *Anax imperator* Leach, 1815, preying on a coenagrionid larva. The labial palps are used for handling/securing the prey, while the mouthparts cut off pieces. *Photo by Karsten Grabow.*

larva depends on stimuli from mechanoreceptors on its legs, antennae, and mouthparts. Some larvae seem to combine these modes, being visual/active, visual/sedentary, tactile/active, and tactile/sedentary (Suhling et al., 2005). The functional response of Odonata may vary considerably between species (e.g., Pickup and Thompson, 1984). Factors affecting the feeding rate may be prey size, prey abundance, presence of other predators, prey handling time, and temperature (Gresens et al., 1982).

Adult Foraging Behavior

Adult Odonata are visual predators depending on their eyesight to capture their prey. While many Zygoptera capture flying as well as sitting prey (e.g., aphids from leaves or spiders from webs; Corbet, 1999, pp. 354–356), most Anisoptera capture only flying prey. Dragonflies seem to be highly selective to prey size, preferring prey within a species-specific size range (Olberg et al., 2005); larger prey items are usually rejected. Dragonflies are also able to estimate the distance to potential prey items, up to 1 m for *Libellula* and 70 cm for *Sympetrum*. In addition, dragonflies fly directly to the point of prey interception by steering to minimize the movement of the prey within the same cluster of ommatidia, as observed in *Erythemis simplicicollis* (Say, 1839), and *Leucorrhinia intacta* (Hagen, 1861) (Olberg et al., 2000).

Dispersal and Migration

One of the probably most relevant and least understood mechanisms in Odonata is dispersal. Because Odonata are accomplished fliers, they are usually supposed to be good dispersers. For the same reason it is, however, difficult to track them by direct observation, and quantitative records other than short-range movements are rare (Corbet, 1999, p. 383). In the stream-dwelling *Coenagrion mercuriale* (Charpentier, 1840), in England, lifetime movements may cumulate to only a few hundred meters, which is supported by molecular genetics (Watts et al., 2007). Such unexpectedly limited dispersal may in fact be relatively common in, for instance, mountain-stream species or in highly fragmented populations. In Zygoptera, the other extreme is *Ischnura aurora* (Brauer, 1865), which disperses by rising almost vertically into the air, where air currents then carry it away. This has enabled it to colonize Pacific Ocean islands (Rowe, 1987).

In Odonata, migration is defined as spatial displacement that typically entails part of (or an entire) population leaving the habitat where emergence took place and moving to a new habitat in which reproduction takes place (Corbet, 1999, p. 384). Migration may be a facultative or an obligate part of the life cycle. Examples of facultative migration events are well known even to the general public in parts of Europe and particularly in Siberia. Such migrations occur in species with strong (up to 100-fold) fluctuation in population density. For example, a 10-year cycle was traced in *L. quadrimaculata* (Haritonov and Popova, 2011).

Obligate migration is typically associated with temporal habitat discontinuity imposed by seasonal drought or cold. In the tropics, seasonal movements of the Intertropical Convergence Zone (ITCZ) cause the seasonality of the rainfalls associated with it. The circumtropical *P. flavescens* travels with the air masses bringing the rains, which enables this species to exploit temporary pools as a larval habitat. It produces one generation in the temporary pools, which leaves the emergence site and does not return. New results indicate that they may fly back to the regions from which their parents once came. Observations from the Maldives and Seychelles imply that *P. flavescens* uses tailwinds to cross the Indian Ocean (Anderson, 2009). Anderson hypothesized a scenario for *P. flavescens*, which, completed in four generations, would cover a total distance of at least 14,000 km aided by alternating monsoons. This cycle would include breeding in equatorial East Africa in October–November, in southern Africa in December–February, and again in East Africa in March–May, before returning to India with the ITCZ and Somali Jet in June–July.

A well-known example of an obligate migrant circumventing cold is *Anax junius* (Drury, 1773), a tropical-centered species that, however, breeds in most of North America and often appears at high latitudes well before local emergence occurs, while southwards movements occur in September–October. The migratory patterns and apparent decision rules of *A. junius* are strikingly similar to those proposed for songbirds (Wikelski et al., 2006). Similarly to *A. junius*, the ITCZ-migrant *Anax ephippiger* (Burmeister, 1839) enters the temperate zone in Europe (Corbet, 1999, p. 412) from its main reproduction areas centered around the Sahara, with wanderers being recorded as far north as Iceland, where no dragonflies occur continuously. However, the arrivals in central and northern Europe seem to be rather irregular and governed by certain wind events (Burbach and Winterholler, 1997).

Habitats

Generalists versus Specialists

Odonata occur in almost all types of freshwater habitats, and a few species are even terrestrial or occur in quite saline habitats. Many are restricted to certain habitats, such as forest streams, acidic waters, or even tree holes. Among the most important habitat conditions for odonate larvae is the presence or absence of predators, particularly fish, which will be discussed below. An example of a species occupying a highly restricted habitat is *Aeshna viridis* Eversmann, 1836, in Europe, which requires the leaves of water soldier *Stratiotes aloides* (Linnaeus, 1758), for oviposition and as a larval shelter. The distribution and patch area of this plant seems to restrict the odonate population size (Suhonen

et al., 2012). By contrast, many species reproduce in a wide variety of habitats. Such "opportunistic" species are usually widespread and can be found in almost all species assemblages of their distribution range. *Crocothemis erythraea*, which colonizes various types of habitats, is the most common African odonate, and it is currently expanding its range northward through Europe. Its Asian counterpart, *Crocothemis servilia* (Drury, 1773), became invasive after translocation of larvae with aquarium plants to Florida, Cuba, and Hawaii. Many *Ischnura* species are also widespread opportunists, for instance, *I. elegans* in the Palearctic and *I. senegalensis* in the Paleotropics.

Habitat Selection

While the relatively sedentary larval stage is usually confined to a specific body of water, the mobile adult may use a variety of structures in the landscape. The adult may spend the time preceding maturation far away from the breeding habitats in forests or even on mountain tops. Large Aeshnidae often hunt along forest fringes. Thus, a larger part of the landscape matrix may be important to an odonate, as exemplified in Figure 35.21. The selection of the "right" habitat for reproduction may encompass various elements; viz landscape type or macrohabitat (or "biotope," cf. Corbet, 1999), type of water body (river, lake, etc.), and oviposition habitat. Habitat selection is a process of successive steps, of which the first two, selection of macrohabitat and water body type, are mainly achieved by visual

perception (Wildermuth, 1994). The selection of the oviposition habitat may also involve tactile and thermal perception. Polarized light is one of the cues used to identify the aquatic habitat from a distance (Bernath et al., 2002). The growth form of plants and their distribution in the water are also clues used in habitat selection (Wildermuth, 1994).

Many dragonflies require plants in their habitat because they oviposit in plant tissue (endophytic), such as most Zygoptera and Aeshnidae; or they glue the eggs to plants (epiphytic), such as some Libellulidae, e.g., *B. lacustris*. The plants used for oviposition may be very specific, as described above for *A. viridis*; but most species use a wider variety of plants. In most cases the plants are submerged and often with relatively soft tissue, but some species also oviposit in reeds and even in the bark of trees, such as *C. viridis* (Vander Linden, 1825). Other species with a well-developed ovipositor may, however, also oviposit in dead plant material, in wet mud, such as *A. ephippiger*, or in small cracks of stones, such as *Notoaeschna sagittata* (Martin, 1901). Cordulegastridae lay into the sediment of streams and rivers. All Gomphidae and most Libellulidae lay their eggs in the open water or sometimes on land and are, therefore, less restricted in oviposition site selection.

Microhabitat Occupancy by Larvae

Odonate larvae use various types of microhabitat, which may be quite species specific. For instance, most gomphid larvae are burrowers that are segregated by the use of
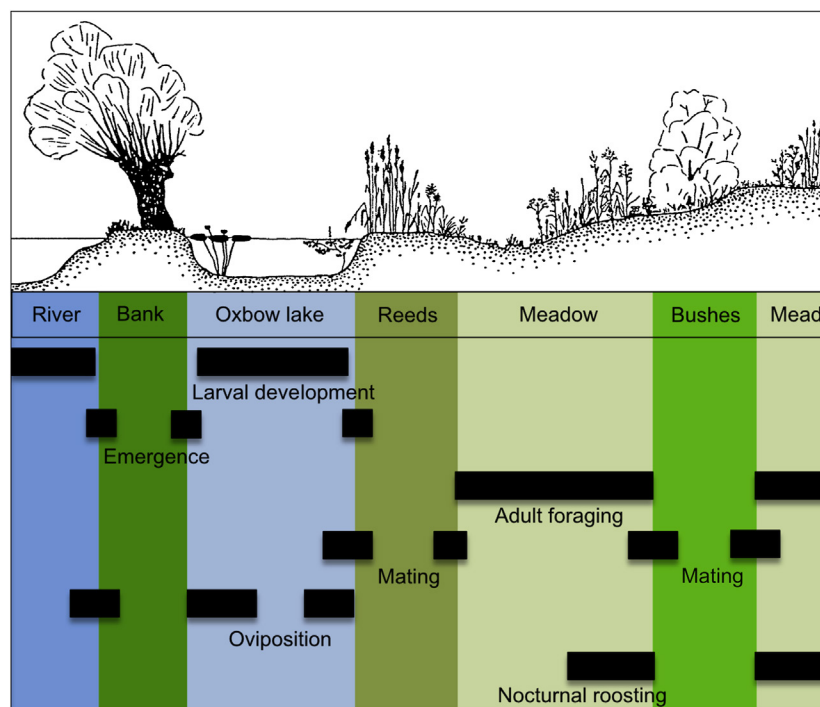

FIGURE 35.21   Use of various structures within the habitat, here a river floodplain, during successive stages in the life cycle of *Platycnemis pennipes* (Pallas, 1771)**.** *Altered and redrawn from Martens (1996), with permission.*

different substrates, such as sand or mud, in which they burrow. Others hide among debris, or among submerged vegetation or tree roots. Corbet (1999) distinguished four types of larvae based on microhabitat occupancy, body shape, and behavior (mainly use of the legs) (Figure 35.22).

1. Claspers exhibit thigmotaxis, i.e., they press and secure their body to a substrate (twigs, stones, etc.). The larvae of many running water Aeshnidae, e.g., *Boyeria* MacLachlan, 1896, live among woody detritus and roots or between stones. *Umma* Kirby, 1889, and *Zygonyx* Selys in Hagen, 1867 (Figure 35.22(a) and (b)), in addition to strong thigmotaxis, have flattened femora, which may also be a morphological adaptation to currents.

2. Sprawlers use their long legs to support the body on or in a matrix, usually detritus or submerged vegetation. This group includes many Aeshnidae, such as *Anax* (Figure 35.22(c)), most Zygoptera (Figure 35.22(d)), and many Libellulidae (Figure 35.22(e) and (f)). Some sprawlers are active in open water. *Pantala flavescens* (Figure 35.22(e)) can swim by jet propulsion for relatively long distances during foraging, a behavior also shown by *Anax*. Some Lestidae, such as *Archilestes grandis* (Rambur, 1842), may float near the surface for long periods.

3. Hiders cover their body with detritus or sit in cavities between stones. The larvae that live among leaf litter have often dorsoventrally flattened bodies and particularly long legs, which they spread out sideways such
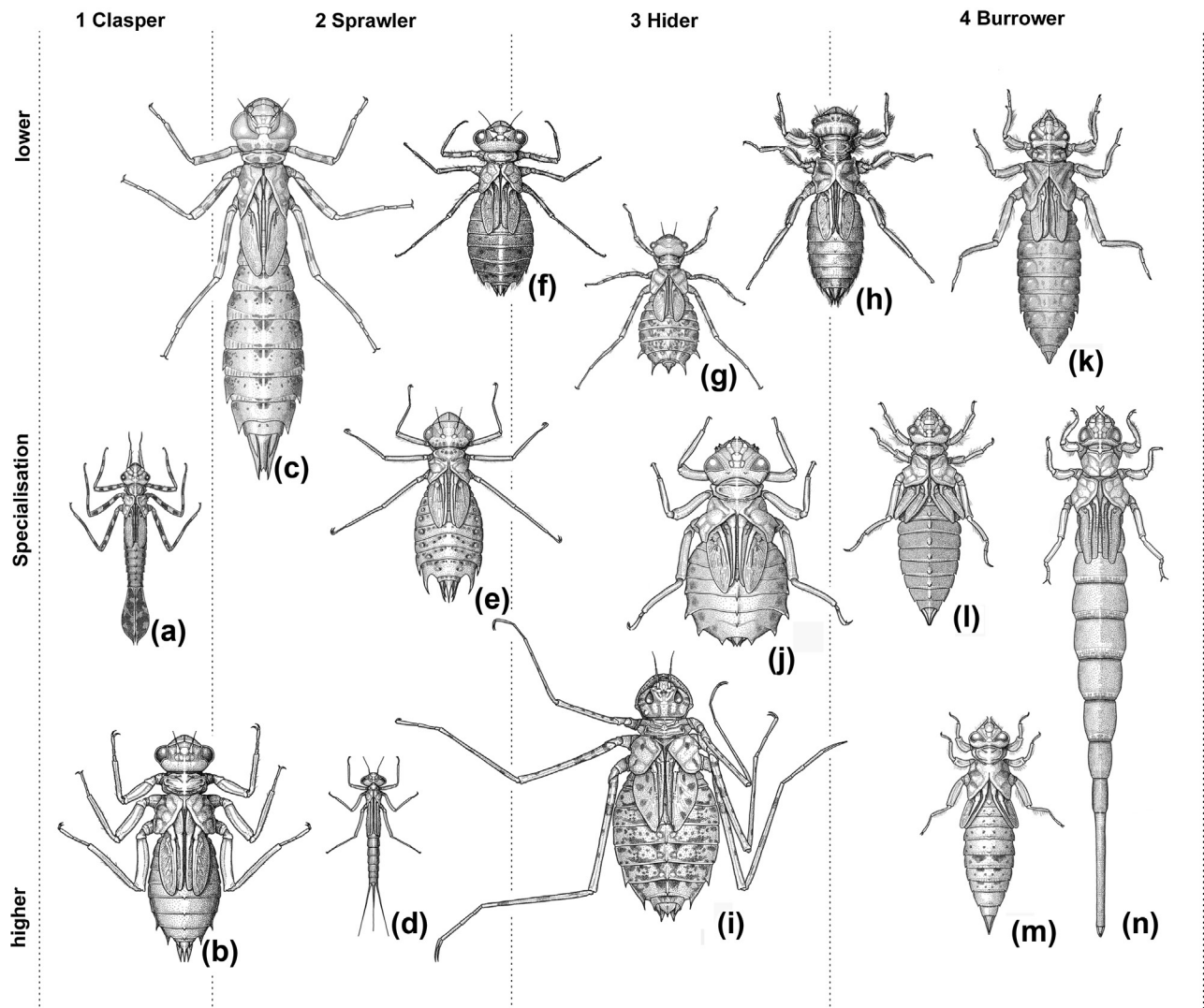

FIGURE 35.22　Body shapes and microhabitat types among Odonata. The graphic indicates the position of various body shapes along a gradient from clasper to sprawler, hider, and finally burrower. Drawings on the lines imply an intermediate position. (a) *Umma* (Calopterygidae); (b) *Zygonyx* (Libellulidae); (c) *Anax* (Aeshnidae); (d) *Ischnura* (Coenagrionidae); (e) *Pantala* Hagen, 1861; (f) *Diplacodes* Kirby, 1889; (g) *Brachythemis* Brauer, 1868; (h) *Orthetrum* (e–h Libellulidae); (i) *Phyllomacromia* (Macromiidae); (j) *Gomphidia* Selys, 1854; (k) *Notogomphus* Hagen, 1858; (l) *Onychogomphus* Selys, 1854; (m) *Paragomphus*; and (n) *Neurogomphus* Karsch, 1890 (j–n Gomphidae). *Drawings by Ole Müller.*

as many Macromiidae (Figure 35.22(i)), Corduliidae, Libellulidae (Figure 35.22(g)), and some Gomphidae (Figure 35.22(j)). The latter may have a more bulky abdomen; both groups have a rounded abdomen in dorsal view.

4. Burrowers have a compact body and execute digging movements with their legs, which results in the body being hidden in the sediment. Most Gomphidae, all Cordulegastridae, Chlorogomphidae, and some Libellulidae belong to this type. Some gomphid larvae are elongate with long breathing tubes, up to half their body length, allowing them to breathe in water when deeply burrowed in the sediment. Generally, the length of the hind legs indicates where a larva is living: shallow burrowers in finer substrates have longer legs (as in Figure 35.22(k)), whereas species digging in coarse substrates (Figure 35.22(l)) and deep burrowers (Figure 35.22(n)) have shorter legs relative to the abdomen. Figure 35.22(m) represents a specialized "sand-swimmer" that can dwell in shifting loose sand. This life style has developed independently in Old World *Paragomphus* Cowley, 1934, and New World *Progomphus* Selys, 1854.

The four categories are not distinct groups, since there are intermediate forms. For instance, *Orthetrum* Newman, 1833, larvae (Figure 35.22(h)) are camouflaged by detritus and tend to hide, but may also exhibit digging movements and cover themselves with sand—they may be seen as intermediate between hiders and burrowers.

Lotic Waters

River systems serve as a habitat for a wide variety of Odonata; 66% of all African and 64% of all Australasian species are riverine (Clausnitzer et al., 2012; Kalkman and Orr, 2012). However, this does not mean that all of them are truly lotic. In many cases the larval habitat is in lentic parts of the river as between reeds or in pools, and such species avoid the current. If they live in exposed habitats, such as many *Calopteryx* larvae in plants floating in the current, they possess thigmotaxis and low locomotory activity. Strong thigmotaxis is known in *Zygonyx* larvae (Figure 35.22(b)) that often adhere to driftwood or stones in the very strong current of rapids and even waterfalls. Even most gomphids, which are usually perceived as lotic species, live burrowed in the sediment and, by doing so, avoid the current. When placed on the sediment surface, *G. vulgatissimus*, dwelling in slow current reaches, accelerates digging with increasing current. *Ophiogomphus cecilia* (Fourcroy, 1785), which lives in reaches of faster currents, immediately starts burrowing rapidly at any current velocity (Suhling and Müller, 1996, p. 97ff.). *Gomphus vulgatissimus* is not well-suited behaviorally to cope with current. When accidentally entering the drift, it becomes rather immobile and thus drifts

away. In contrast, larvae of *O. cecilia* immediately swim toward the substrate and start digging; reduced activity is probably also one of the traits to avoid current. Gomphidae that live in upper reaches and more in the stream channel are less active than species of lower reaches; this may allow them to avoid exposure to the current (Suhling and Müller, 1996, p. 104).

Most lotic species have in common a body that is more compact than those of lentic water species. The cuticula seems to be thicker and is sometimes strengthened by dorsal knobs or hooks on the abdomen, which may serve as a protection against pebbles being tossed around by the current or as hydrodynamic elements that stabilize the larvae's position in the current. Interestingly, anisopteran larvae that are dorsoventrally flattened are usually not found in strong currents. Their body shape seems to be an adaptation to a burrowing or hiding life style.

Temporary Habitats: Coping with or Avoiding Drought

Living as an aquatic animal in temporary waters means having to cope with, or circumvent, the harsh conditions of the dry season. Species that reproduce in temporary waters need specific strategies to survive. In Odonata, several cases of siccatation (i.e., surviving drought, cf. Corbet, 1999, p. 586) are reported in all life stages. Some larvae may survive long periods of complete habitat desiccation. Larvae of at least some species of burrowing gomphids and libellulids can survive in moist sand. Larvae of the Australian aeshnid *Telephlebia brevicauda* Tillyard, 1916, hide in wet detritus. Siccatation in the egg stage is very common as in most species of *Lestes*, which enables them to survive several months (and perhaps even a few years) of drought. Also some Libellulidae, such as the Oriental *Potamarcha congener* Rambur, 1842, survive the dry season in the egg stage; the development is triggered by low oxygen content when the pond is refilled with water (Miller, 1992). The eggs of *S. sanguineum* seem to be protected against drought and frost by their thick exochorion (see previous discussion of egg morphology).

Interestingly, dry-season survival of the aquatic stages appears to be uncommon in species living in arid regions; most of these species develop directly and require open water. The main trait seems to be rapid development that allows them to emerge before the habitat dries out (Johansson and Suhling, 2004). The temporary pond specialist *P. flavescens* completed larval development in Namib Desert ponds in 38 days; it is probably able to make it in 30 days. *Crocothemis erythraea*, not a temporary water specialist, needed 49 days in temporary ponds (Suhling et al., 2004). Such rapid development would then be connected with a habitat change in the next generation, for instance to nearby permanent waters or to following the seasonal occurrence of temporary waters as described for

P. flavescens (life cycle type C). Another strategy of temporary water species is to postpone reproductive maturation until the onset of the rainy season (see previous discussion of life cycles). Simply avoiding drought by spending the dry period as adults may be the most common habit in the Odonata of temporary waters.

Acidic Ponds and Lakes

Experiments on *A. junius* have shown that eggs of this species can survive at a pH as low as 3, although the survival rate is only 10% (Punzo, 1988). Dragonflies survive better than fish and many other invertebrates in acidic environments. Many northern temperate bog and tropical blackwater species possess a tolerance to living in environments with fairly low pH levels. Some species, particularly in the circumboreal genera *Leucorrhinia* Brittinger, 1850, *Aeshna*, and *Somatochlora*, are well adapted to naturally acidic waters, e.g., peat bogs, where living among the *Sphagnum* shoots offers protection against predation as well as ample food (cladocerans, which thrive in bog pools). The growth of these species is, however, faster in waters with a normal pH (Sternberg, 1990). But at northern latitudes, bog pools also warm up fairly rapidly and have high daytime temperatures, enabling their inhabitants to keep a faster growth rate (Sternberg, 1990). Odonata are often the top predators in acidic waters.

Saline Waters

Odonata are freshwater organisms but many species are tolerant to some degree of salinity. Only a few species are reported from very salty water, but the situation is different with moderate levels of salinity. In experiments *Ischnura heterosticta* (Burmeister, 1839), developed faster in waters with low salinity (5–20 mS/cm) than in freshwater (Kefford et al., 2005). This is consistent with the observation that many species live in the Baltic Sea (salinity 0.3–c. 1%), and 10 of them are confirmed to breed in the seawater (Henriette Persson, personal communication). Some of these, e.g., *O. cancellatum*, are well-known generalists; but others, like *Brachytron pratense* (Müller, 1764), have a much narrower habitat range when occurring in freshwater. Rock pools and coastal lagoons are other brackish water habitats that are colonized by dragonflies. In Northern Europe, *Aeshna grandis* and *L. quadrimaculata* are common species in these habitats, while *L. congener*, *L. quadrimaculata*, and certain *Sympetrum* species are abundant in rock pools in North America (Catling, 2009). *Erythrodiplax berenice* (Drury, 1773), is truly marine; it occurs in tidal marshes and in mangroves at the east coast of North America, the larvae being able to tolerate large variations in salinity (Dunson, 1980). Thus, it seems as if many Odonata, at least in the families Coenagrionidae, Aeshnidae, and Libellulidae, can tolerate low levels of salinity. This gives them an advantage

in being able to also utilize more extreme and transient environments.

Forest and Shade Habitats

The effect of shade on the occurrence of dragonflies varies. In the tropics, many species are forest dwelling, and shade is a relevant factor in habitat segregation for species occurring in tropical running waters (Dijkstra and Lempert, 2003). By contrast, invasive trees overgrowing naturally nonshaded streams repelled various Anisoptera (Remsburg et al., 2008). In the temperate zone a minority of dragonflies, such as *A. cyanea*, tolerate deep shade and may breed in very shady forest ponds.

Very Small Habitats

The smallest aquatic habitats where Odonata reproduce are probably phytotelmata. A variety of species breeds in water-filled tree holes and cavities of bromeliad plants (Corbet, 1983; Orr, 1994), among them the huge coenagrionid damselflies formerly placed in Pseudostigmatidae. Most of these species have to be shade tolerant. The habitats are so small that only a single larva is usually able to survive due to heavy inter- and intraspecific competition and predation (Fincke, 1999). Also in the temperate zone some species, however, breed in very small water bodies, such as tiny pools in peat bog, an example being *Somatochlora alpestris* (Selys, 1840). Special cases are the self-burrowed cavities of Petaluridae in bogs, seepages, or along streams. These cavities, where the larvae spend most of their lives, reach down to the water level, but foraging mainly occurs on land (Rowe, 1987).

Terrestrial Habitats

Odonates that live in very small habitats are especially likely to leave the water episodically. The spring-dwelling larvae of *Cordulegaster bidentata* Selys, 1843, may hunt epigaeic (soil surface dwelling) arthropods on land at night. But some odonates, among them mainly Zygoptera, spend their entire development time in terrestrial microhabitats. Most of them occupy moist ground litter, often, but not necessarily, in the vicinity of aquatic habitats (Corbet, 1999). Species that show advanced terrestrialism, such as the Hawaiian *Megalagrion amaurodytum* Perkins, 1899, climb out of the water when placed into it. This is also true of the petalurids *Phenes raptor* Rambur, 1842, and *Tanypteryx pryeri* (Selys, 1889).

Biotic Interactions

In the food web of freshwater habitats, odonate larvae occupy intermediate to top positions, mainly depending on the presence or absence of fish as predators. In lakes and

rivers, where fish are common, odonates occupy an intermediate position in the food web, while in fish-free lakes and streams, they may be the top predators. The effects of fish on the abundance of dragonfly larvae in a lake may affect the terrestrial plant community surrounding the lake via predation by adult dragonflies on pollinating insects (Knight et al., 2005).

Predation

Predators of Imagines

Adult dragonflies are most susceptible to predation during their emergence and maiden flight, when their flight ability is poor or nonexistent. Predation during annual emergence causes up to 28% mortality (Jakob and Suhling, 1999). Various predators have been observed preying on emerging Odonata, particularly birds and ants, but also more exotic ones such as flatworms and young crocodiles (Suhling and Müller, 1996, p. 41ff.; Corbet, 1999, p. 329).

Mature Odonata are often captured by predators when distracted, e.g., during courtship or reproduction (Rehfeldt, 1992). They may then end up in cobwebs, or get caught by other ambush predators, such as mantids or frogs (Figure 35.23). Anisopterans often prey on zygopterans and may even cause sharp, temporary population declines. The extremely fast and agile Anisoptera seem at low risk during normal flight, some exceptions being other Anisoptera and a few birds with excellent flight abilities. Anisoptera made up 46% of the prey of nestlings of European bee-eaters, *Merops apiaster* (Linnaeus, 1758) (Krebs and Avery, 1984).

Predators and Antipredation Traits of Larvae

Apart from other Odonata, the main predators of odonate larvae are probably fish, which play an important role in shaping the odonate community structure of lakes, as clearly demonstrated in studies of *Enallagma* spp. in North America (reviewed in Johnson, 1991). Some odonate species behave cryptically, for example, by reducing movement; this increases survival chances when fish are present. Others are quite active and may escape invertebrate predators by swimming away. In fish-free habitats, newts and certain large invertebrates prey on odonate larvae; the latter include dytiscid beetles (adults and larvae), crayfish, and belostomatid bugs. Moorhens, ducks (Horváth et al., 2012), egrets, and herons feed on odonate larvae (Samraoui et al., 2012), but the extent to which water birds in ponds and wetlands impact odonates has not been adequately quantified.

Odonate larvae have developed various morphological and behavioral features to reduce the risk of fish predation (Table 35.2). These traits may be fixed and, thus, occur both in the presence and absence of a predator, or they may be flexible in response to predators, as demonstrated in five central European species (Wohlfahrt et al., 2005). Larvae of *Platycnemis pennipes* behaved cryptically independently of the presence of fish. The response of other odonates depended on the fish species, and it varied among species of dragonflies. In a test using three fish species, *C. puella* (Linnaeus, 1758), larvae reduced their activity in the presence of any of the three fish species (*Perca fluviatilis* Linnaeus, 1758, *Gobio gobio* Linnaeus, 1758, and *Scardinius erythrophthalmus* Linnaeus, 1758), whereas the bottom-dwelling
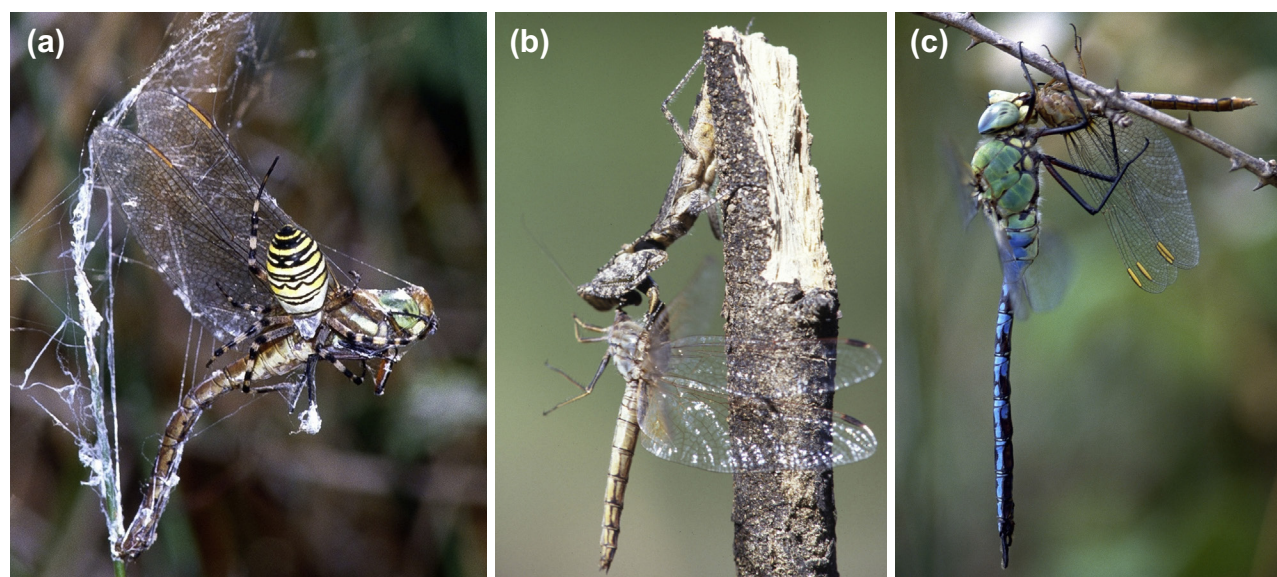

FIGURE 35.23   Predators of adult dragonflies. (a) *Aeshna isoceles* (Müller, 1776), caught in the web of aspider, *Argiope bruennichi* (Scopoli, 1772); (b) *Trithemis kirbyi* Selys, 1891, female caught by a mantid, probably of the genus *Tarachodes*; and (c) immature *Orthetrum coerulescens* (Fabricius, 1798), caught during maiden flight by another dragonfly, *Anax imperator*. *Photos by FS.*

TABLE 35.2 Features of Larval Morphology, Ecology, and Behavior Serving to Reduce Predation Pressure

Feature		Expressions
Crypsis	Color	• Close resemblance to microhabitat background, i.e., being greenish among vegetation or black in mud or between dark detritus • Ability to change color after translocation to another microhabitat
	Pattern	• Dark spots on a pale brown background mimicking the pattern of a mixture of different sediments, e.g., in Macromiidae • Transverse bands of contrasting dark and pale stripes in younger stadia of e.g., *Anax* spp. resembling the patchwork of light and shade near the water surface
	Camouflage	• High density of setae on most parts of the body creating a camouflage effect by collecting fine detritus
	Habitat	• Hiding in dense vegetation (Thompson, 1987) • Burrowing in suitable (soft) substrate (Suhling and Müller, 1996, p. 118)
	Behavior	• Thigmotaxis (see above) (Corbet, 1999, p. 150) • Nocturnal circadian rhythm (Pierce, 1988) • Low locomotory and foraging activity (Johnson, 1991)
Escape	Thanatosis	• Feigning death by immobilization and "unnatural" posture when attacked (Wildermuth, 2000) (Figure 35.24(a))
	Swimming or walking	• Broad caudal appendages to increase swimming speed (McPeek, 2000) • Jet propulsion as a rapid escape mechanism (Corbet, 1999)
	Autotomy	• Deliberate loss of caudal appendages (Stoks, 1999)
Defense	Attack or threat display	• Use of the spiky pyramid to "sting" predators by species with a flexible abdomen (e.g., aeshnids). • Sound production in *Epiophlebia*?
	Spines	• Abdominal spines in Anisoptera; the combination of long dorsal and lateral spines is most effective in warding off fish (Johansson and Mikolajewski, 2008) (cf. Figure 35.24(b))

L. depressa altered its activity only in presence of the likewise bottom-dwelling *G. gobio*. Two other odonates, *Lestes sponsa* (Hansemann, 1823), and *S. striolatum*, did not respond to any of these fishes.

Intraguild Interactions

Several investigations have shown that the composition of a dragonfly community is strongly affected by predation within the guild (Johansson, 1993), particularly if larger predators are missing. Ecologically relevant rates of intraguild predation are usually caused by size differences (Benke, 1978), which may be caused for instance by different seasonal phenology (Wissinger, 1992). In tree-hole communities in the Panama rainforest, the sequence of colonization of the habitat largely controls which species survives ("priority effect") (Fincke, 1999). In ponds in the Namib Desert, three factors determine the composition of the community: intrinsic growth rates (Johansson and Suhling, 2004), priority effects (Padeffke and Suhling, 2003), and the seasonal immigration of obligate migrants (mainly *P. flavescens*, which temporally dominates the community due to its extremely rapid growth).

Intraspecific Interactions

Populations of larvae are affected by several density-dependent effects, among them cannibalism (Van Buskirk, 1989). Food supply and population density strongly affected survival as well as timing of, and weight, at emergence in damselflies, with intraspecific interference causing a more even distribution of the larvae (Anholt, 1990). Spacing is surely caused by agonistic behavior among conspecifics; this usually features ritualized, protracted display and culminates in the loser departing. Often the loser remains unharmed, but injures and killing may occur. Larvae of many zygopterans, e.g., *Xanthocnemis zealandica* (MacLachlan, 1873), show distinct postures mainly of their caudal appendages during agonistic display to exclude rivals from perches (Rowe, 1987). Agonistic display in Anisoptera is less distinct than in Zygoptera since it often involves strikes with the labium, which makes it difficult to distinguish from foraging.

Abiotic Limitations and Biotic Interactions

The community structure of dragonflies is governed by a combination of biotic factors, the abiotic environment, and traits of odonate species. A good example is the *Lestes*
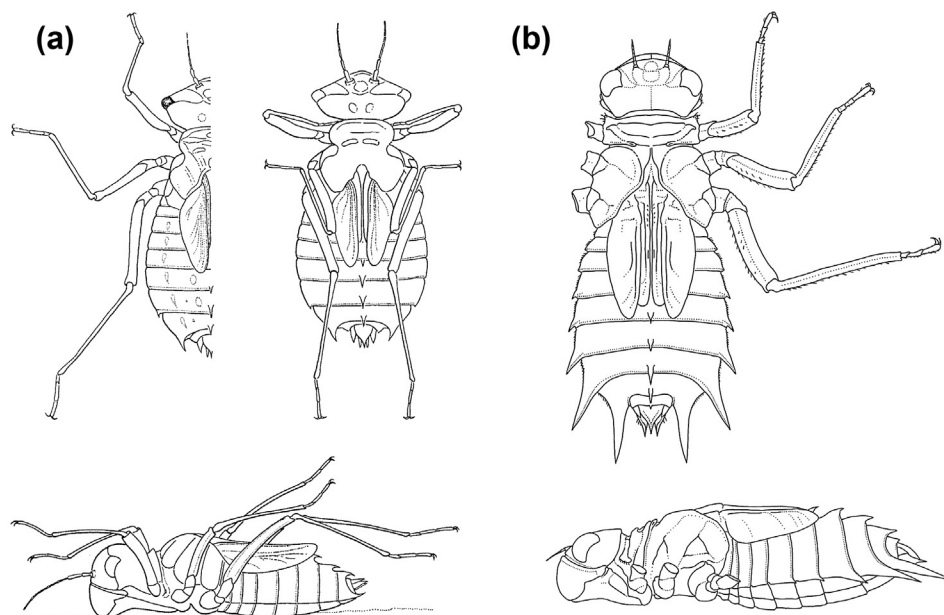
FIGURE 35.24   Illustrations of two antipredation traits. (a) Thanatosis in *Somatochlora flavomaculata* (Vander Linden, 1825); a last instar larva shown in normal sitting posture (left) and in thanatosis after a simulated attack (right and below) *Drawing by Hansruedi Wildermuth*; and (b) dorsal and very pronounced lateral abdominal spines of the riverine *Zygonoides occidentis* (Ris, 1912), in lateral and dorsal view *Drawing by Ole Müller*. The spines may serve as a defense from fish and as a means of preventing the larva from being carried away by strong currents (possible spoiler function of downward pointing spines).

assemblage in the northeastern United States (cf. Figure 35.25). The duration of larval development shapes the ability of species to cope with seasonal drying, thereby excluding perennial-water *Lestes* from temporary ponds, but also temporary-pond species from vernal ponds that dry up earlier in the year than temporary ponds. Differences in the timing of hatching generate size differences between the species, causing the exclusion of temporary-pond *Lestes* from perennial water bodies through asymmetric intraguild predation. Predation by large dragonfly larvae excludes the vernal pond specialist *Lestes dryas* Kirby, 1890, from temporary ponds. Finally, differential vulnerability to large dragonfly larvae (mainly *Anax*) and fish shapes the reciprocal dominance of the two perennial-water species, *Lestes eurinius* Say, 1839, and *Lestes vigilax* Hagen in Selys, 1862, in fishless and fish-containing water bodies (Stoks and McPeek, 2003).

Parasitism and Other Interactions

The most conspicuous parasites on Odonata belong to three families of water mites (Hydracarina), which are ectoparasites on the bodies and wings of imagines. The larvae of *Arrenurus* spp. attach to F−0 larvae during emergence and remain on the imagines until returning to water. Single dragonflies may be infested by several dozen water mites of multiple species. The prevalence of infestation in the odonate populations may be up to 100%, and severe effects are reported (reviewed by Rolff (2001)). Imagines

of Ceratopogonidae (biting midges) suck hemolymph from the wings of Odonata (Wildermuth and Martens, 2007). Odonate larvae may be hosts of gregarines and serve as intermediate hosts for several Trematoda and Cestoda. The final hosts are amphibians, birds, and mammals, including occasionally humans in countries where dragonfly larvae are eaten (Corbet, 1999). Various sessile organisms, such as Simuliidae (black flies) and Bivalvia, may colonize dragonfly larvae. *Dreissena polymorpha* mussels attached to *Macromia illinoiensis* Walsh, 1862, decreasing the prey capture ability of the latter (Fincke and Tylczak, 2011).

Distribution and Diversity

Diversity Patterns

Today's patterns of dragonfly diversity correspond largely with the present climatological zones. As a general rule, diversity increases with temperature and precipitation, with most species occurring in tropical rainforest (Kalkman et al., 2008; Clausnitzer et al., 2012). Within the temperate region of the northern hemisphere, the highest diversity occurs in the zones with broad-leaved forest. The taiga and tundra are relatively species poor, and to the south diversity decreases with decreasing precipitation, with notable gaps in arid and desert regions. This pattern is especially evident in Europe and Central Asia but also in North America. In the Eastern Palearctic, the temperate broad-leaved forest merges more gradually into the rich Oriental fauna. In the tropics, diversity is affected by the
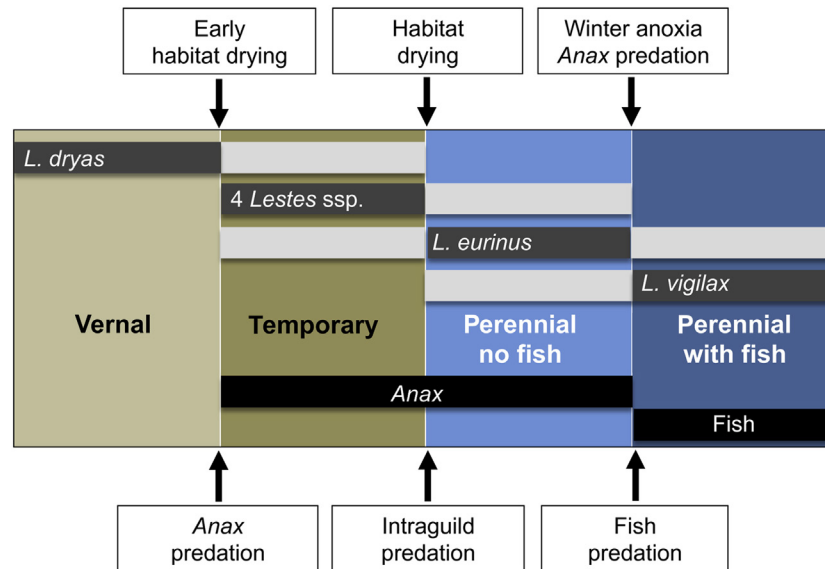
FIGURE 35.25   Schematic overview of the habitat gradient colonized by *Lestes* species in northeastern United States in relation to pond drying and predation. Coded bars (dark: species abundant, light: rare) indicate the ranges of the taxa, and arrows show the ecological forces that limit a species' range along the gradient. The four species in temporary ponds are *Lestes congener* Hagen, 1861, *Lestes disjunctus* Selys, 1862, *Lestes forcipatus* Rambur, 1842, and *Lestes rectangularis* Say, 1839. Arrows below the species bars represent processes that restrict a species to the less permanent side of the gradient, and arrows above represent processes that restrict a species to the more permanent side of the gradient. *Altered and redrawn from Stoks and McPeek (2003), with permission.*

amount of rainfall and its seasonal distribution. Areas with high precipitation throughout the year are richest, while those with a distinct dry season (e.g., monsoon climates) are relatively poor. Areas with tropical forest and/or mountains are in most cases relatively species rich, partly because they offer a wide array of aquatic habitats and partly as they often coincide with regional climatic refugia (Oppel, 2005; Orr, 2006; Clausnitzer et al., 2012). The relative long-term stability of forest habitats (also in the short term, the limited seasonality), which provides opportunities for animals with a specialist lifestyle, might also explain the high diversity of tropical odonates. Figure 35.26 illustrates the pattern of biodiversity on a continental scale.

The diversity patterns shown by the suborders Anisoptera and Zygoptera largely coincide with that of Odonata in general. There are, however, great differences in diversity patterns at the family level, with 19 of the 39 families being confined to the tropics (Table 35.1; Figure 35.27). Generally, the more species-rich families have larger distributions, and families with a small distribution mainly inhabit running water. Among them, three of the four largest families (Coenagrionidae, Libellulidae, and Aeshnidae), contain most of the widespread or ubiquitous odonate species. Together with Lestidae, they are dominant in unshaded habitats with standing water (both artificial and natural; e.g., in savannas). Aeshnidae, Coenagrionidae, and Libellulidae include the species possessing the greatest dispersal capacities—those with distributions spanning more than one continent and the vast majority of species found on isolated islands. Species-rich and widespread families inhabiting running

water include Gomphidae (worldwide), Calopterygidae (worldwide except Australia), and Platycnemididae (Africa and Eurasia to New Guinea). Although these families are widespread, their genera and species are not; and in contrast to those associated with standing waters, very few genera occur in more than one continent.

Range Shifts due to Climate Change

The impact of climate change on dragonflies has been documented in numerous papers. It includes changes in range, flight period, life histories, and species composition (Hassall and Thompson, 2008). It seems that, at least in the temperate part of the world, climate change has become one of the most important driving forces behind distributional change in dragonflies. Well-documented examples of this are known from North America, Japan, and especially Europe, where many southern species are expanding. It is likely that climate change is also impacting dragonflies in other parts of the world, but in many areas information is scant or weather extremes are so frequent that it is difficult to relate range changes directly to large-scale climate change. Information on the tropics is especially sparse, although Hoffmann (2010) presented some indications that changes in range and flight period are taking place in western Peru. In Europe the increased temperature has resulted mainly in the expansion of ubiquitous species of standing water (Ott, 2010). For instance, in Scandinavia, *Anax imperator* has shifted its range northward by almost 1000 km within
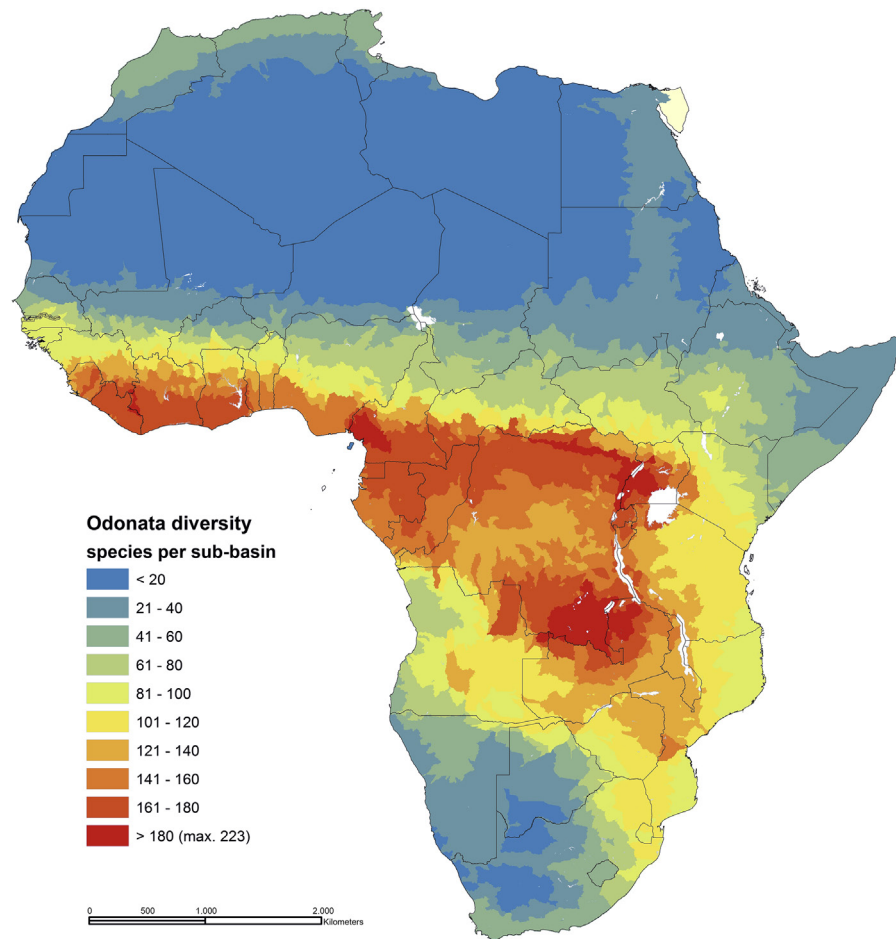
FIGURE 35.26   Distribution of dragonfly diversity in continental Africa, mapped as the number of species per basin *(Updated from Clausnitzer et al. (2012).).* Diversity is lowest in desert areas, with a steep increase in species richness where the desert ends and a further increase where the rainforest begins especially where these coincide with highlands. *Original by Jens Kipping.*

11 years (Flenner and Sahlén, 2008). Evidence of strong negative impact of climate change on dragonflies is lacking, although local examples of desiccation of bog habitats and streams have been published.

Conservation Status and Biotic Indicators

Dragonflies are increasingly used as indicators of aquatic ecosystem quality and biodiversity as they can be identified relatively easily and, in many cases, have well-known habitat requirements. Monitoring of biological water quality in the tropics is often difficult due to the large number of species involved, and in such areas dragonflies may serve as convenient indicators. The Dragonfly Biotic Index—a compound index based on geographical distribution, conservation status, and ecological sensitivity—has been developed for this purpose and is currently applied in tropical Africa and elsewhere (Simaika and Samways, 2009).

A global assessment of the conservation status of a random sample of 25% of all Odonata species showed that about

one species in 10 is threatened by extinction (Clausnitzer et al., 2009). Examples of regions with many threatened species are Sri Lanka, Indonesia, and the Philippines, where many species with small ranges are threatened by large-scale deforestation. The percentage of threatened species is probably higher than currently known. Many of Madagascar's endemics are, for instance, assigned to Data Deficient, but it is likely that a large proportion of them are in fact strongly threatened. Since 2000, a number of regional conservation assessments of dragonflies have been conducted; details can be found in several reports published by the IUCN at the website www.iucn.org/about/work/programmes/species/our_work/about_freshwater/.

The most important causes of decline are usually destruction of aquatic habitats in general, and the canalization of streams and rivers. The main threat in the tropics is deforestation, which destroys the habitat of shade-loving species and through erosion can have a strong negative impact on the aquatic habitats. In addition, invasive species such as trees or fish, have a regional influence. Recent
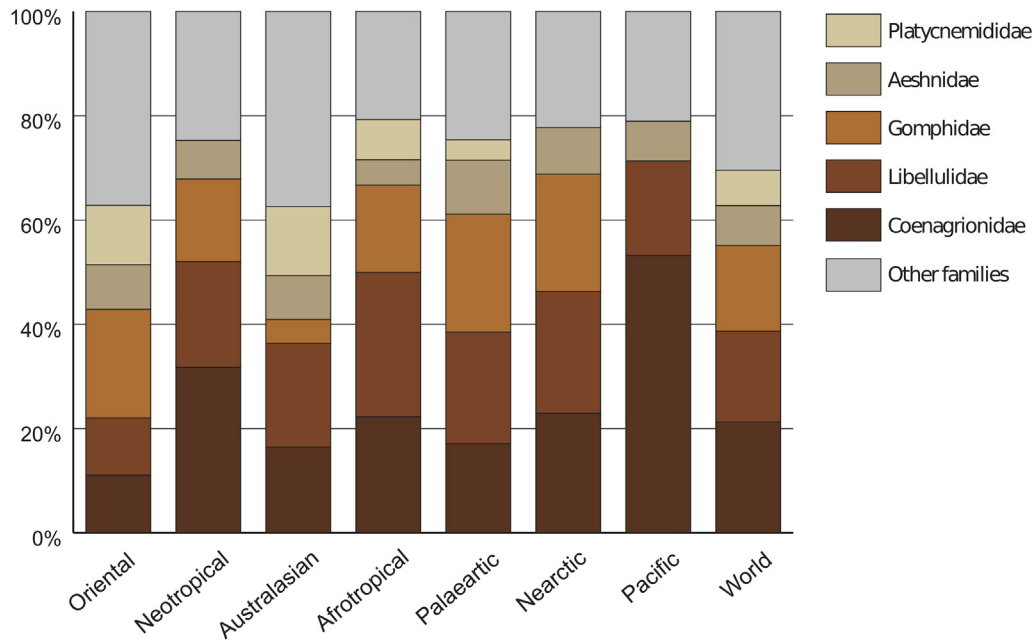
FIGURE 35.27   Percentage of species belonging to different dragonfly families in the seven biogeographic regions. The five largest families are at the bottom with from bottom to top: Coenagrionidae, Libellulidae, Gomphidae, Aeshnidae, and Platycnemididae (note that not all of these are found in all regions). *Original by VK, after data by JT.*

COLLECTING, CULTURING, AND SPECIMEN PREPARATION

Collecting and Sampling

Odonates occur in all types of freshwater habitats, and thus a broad array of habitats need to be sampled to get a proper overview of an area's fauna. It is necessary to spread the sampling not only across a variety of habitats but also across the season and the day. In temperate areas, a visit in spring, early summer, and late summer is sufficient to find the majority of species in the adult stage. In the tropics, seasonality is mainly governed by the rains, with the highest diversity generally found at the start of the rainy season, although seasonality is poorly studied. It is, however, clear that species favor different times of the year, making it necessary to sample throughout the year.

Sampling of larvae, exuviae, and adults each has its advantages (Raebel et al., 2010). Sampling of larvae and especially exuviae provides certainty that a species reproduces in a habitat, but larvae are generally more difficult to find and identify than adults. Many species of certain families (e.g., Gomphidae, Chlorogomphidae, and Corduliidae) are, however, much easier to find as larvae than as adults, because the adults only visit the water briefly for reproduction. This is especially true of many forest species, whose adults tend to disappear in the canopy. In large parts of temperate America, Europe, and Asia, adults can be identified in the field without collecting, making it easier to involve volunteers. Here, observing adults is the most convenient method to collect occurrence data. In the tropics, collecting is nearly always needed for a correct identification, and many larvae cannot be identified to species level at present.

Larvae are collected in the same way as most aquatic invertebrates. A hand net with long handle is the most flexible tool for probing different microhabitats such as weeds, silt, gravel, roots of riverside trees, patches of leaf litter, mud, or sand. In stony streams, kick sampling is essential to get a good impression of the fauna. Odonata larvae are predators and often occur in lower density than most other invertebrate groups. A targeted search for larvae is, therefore, needed to record all species present. Some sampling techniques (e.g., Surber sampler) can be used to estimate larval density, although this easily leads to underestimation of species where the larvae live between vegetation or roots of trees. Larvae may occur in large densities; estimates of the maximum number of larvae per square meter in various microhabitats in a small stream in southern France ranged from 40 to 275.

For both identification and rearing, it is best to obtain full-grown larvae. These have well-developed wing sheaths with clearly visible venation. Collecting exuviae can be combined with looking for adults. Exuviae should be sought for on banks, boulders, or vegetation, from just above the waterline to a height of about 50 cm, although some larvae will travel several meters from the water to emerge.

Dragonflies prefer vertical substrates for emergence (e.g., plants, tree roots, steep banks, rock faces) but may also be found on horizontal substrates (floating plants, sand banks). Exuviae are often washed away by heavy rain, and searches conducted after a few dry days give the best results; otherwise, try looking below sloping rocks or bridges, were they are sheltered from the rain. As exuviae are nothing more than dried skin, they are fragile and legs easily break off. By splashing some water on them they become softer, less brittle, and hence easier to collect.

Adults can be caught with a large sweep net with an opening diameter of about 0.5 m and a handle length of at least 1 m. The net must be deep enough to fold closed, so the catch cannot escape. Catching adult dragonflies is not always easy and requires some experience. The easiest way to store live dragonflies is in small envelopes in a plastic container. Adults are easiest to collect at their reproduction habitat, where males defend territories and females come to lay eggs. Adults can also be found away from the water, e.g., when roosting and feeding, and some species await the rainy season away from their breeding sites. Adults often congregate at the edges of open areas, such as forest clearings, roadsides, and grassy fields, to feed on insects. Some species (e.g., Gomphidae) are very shy in their breeding habitats and easier to catch in their feeding grounds. Most species prefer warm and sunny weather and are active during the day, with a maximum activity around or before noon. Others, among them many members of the families Aeshnidae and Synthemistidae, are mainly active in the half hour around sunrise and sunset.

The use of environmental DNA, i.e., detection of genetic material from a species by sampling the nonliving environment, has been tested with an 80% detection rate for the European species *Leucorrhina pectoralis* (Charpentier, 1825) (Thomsen et al., 2011). It is possible that this method will develop rapidly, and it may prove to be an efficient method for collecting occurrence data for dragonflies.

Culturing

For groups where the larvae are easier to capture than the adults, rearing is a good method for obtaining identifiable material. Dragonfly larvae are generally easy to rear, although transportation has three problems: drying, drowning, and overheating. To make sure that the larvae remain moist and oxygenated, put them in moist cotton wool or toilet paper with little or no free water and with plenty of air, in a small, closed container. Moss or other organic material can also be used, but may rot. Keeping the larvae in a cool box at 5–10 °C will extend their lifespan. For rearing, place larvae in a tray, basin, or aquarium with water and provide them with some substrate (e.g., sand, plants) and a stick or something similar for emergence. Feed with small aquatic invertebrates (mosquito larvae, cladocerans, etc.); large aeshnids

can be fed with small fish. Another efficient method is to find larvae when they are about to emerge and leave the water (e.g., around midnight in the tropics); then place them in a closed space with sufficient room and substrate for the adult to emerge and spread its wings (e.g., a bucket with twigs covered with a net). Culturing dragonflies over their whole life cycle is difficult and has rarely been successfully practiced, since the agile adults are in most cases too difficult to feed properly. Observations from successful spontaneous reproduction in greenhouses may point the way toward successful cultivations of at least Zygoptera.

Preservation

Larvae can be stored in 70–95% alcohol. In contrast to some other insect groups, the larvae of dragonflies are sturdy and do not easily lose body parts. As they are often rather bulky and initially contain substantial amounts of water, it is advisable to refresh the alcohol a few times. The larvae have a rather thick cuticula through which alcohol penetrates slowly; and in Anisoptera, it is necessary to puncture the body of the larvae a few times with a fine pin, preferably penetrating the gut. Exuviae must be stored dry in small containers that close tightly. They will often be moist immediately after collecting and need to be dried before they are stored.

Drying with acetone is the preferred method to preserve adults, although freshly emerged specimens will crumple and should be stored in 70% alcohol. Note that acetone dissolves some kinds of plastic, especially clear and flexible types like PET. Because acetone replaces the water in the animal's body, it dries very quickly, becoming stiff and sturdy, with relatively little color loss and odor development. Dipping the individual in acetone kills it and makes it limp, which makes it easy to straighten the abdomen and stretch the legs. Fold the wings above the body. Large specimens are preferably injected with acetone with a fine-needled syringe. This may also push out the penis, which in Zygoptera can also easily be extracted with a pin, exposing characters that will be hard to see once the specimens are dry. Simply putting dead dragonflies out to dry is only successful in dry climates. In a moist climate they will become moldy and lose color. Drying by deep freezing is another possible method.

Soak in acetone in an airtight container for at most 24 h (about 12 h is ideal). To avoid spreading of the wings, keep each individual in an envelope or under layers of permeable paper. Lay the specimens out on tissue paper to dry after soaking. A breeze or some sun helps, but specimens may blow away or be affected by bright sunlight and overheating. Beware of potential consumers, especially ants. Depending on the conditions, about 30 min is sufficient for the acetone to evaporate. During fieldwork, specimens can be stored in stamp envelopes or paper triangles in an airtight container.

The collection data (or a field code referring to it) can be written on the envelopes. Add silica gel (with moderation, as shock drying can affect the specimens) to keep them dry and extract additional moisture. Pinned dragonflies take up much space and are easily damaged. For this reason, most collectors prefer to keep them in envelopes. The paper triangle or envelope used in the field can be placed in a larger envelope together with a label containing collection and identification data.

ACKNOWLEDGMENTS

REFERENCES

Anderson, R.C., 2009. Do dragonflies migrate across the western Indian Ocean? J. Trop. Ecol. 25, 347–358.

Anholt, B.R., 1990. An experimental separation of interference and exploitative competition in a larval damselfly. Ecology 71, 1483–1493.

Ando, H., 1962. The Comparative Embryology of Odonata with Special Reference to a Relict Dragonfly *Epiophlebia superstes* Selys. The Japan Society for Promotion of Science, Tokyo.

Banks, M.J., Thompson, D.J., 1985. Lifetime mating success in the damselfly *Coenagrion puella*. Anim. Behav. 33, 1175–1183.

Benke, A.C., 1978. Interactions among coexisting predators – a field experiment with dragonfly larvae. Ecology 47, 335–350.

Bernath, B., Szedenics, G., Wildermuth, H., Horvath, G., 2002. How can dragonflies discern bright and dark waters from a distance? The degree of polarisation of reflected light as a possible cue for dragonfly habitat selection. Freshwater Biol. 47, 1707–1719.

Burbach, K., Winterholler, M., 1997. Die Invasion von *Hemianax ephippiger* (Burmeister) in Mittel- und Nordeuropa 1995/1996 (Anisoptera: Aeshnidae). Libellula 16, 33–59.

Bybee, S.M., Ogden, T.H., Branham, M.A., Whiting, M.F., 2008. Molecules, morphology and fossils: a comprehensive approach to odonate phylogeny and the evolution of the odonate wing. Cladistics 24, 477–514.

Carle, F.L., 1986. The classification, phylogeny and biogeography of the Gomphidae (Anisoptera). I. Classification. Odonatologica 15, 275–326.

Carle, F.L., Kjer, K.M., May, M.L., 2008. Evolution of Odonata, with special reference to Coenagrionoidea (Zygoptera). Arthropod Syst. Phylogeny 66, 37–44.

Catling, P.M., 2009. Dragonflies (Odonata) emerging from brackish pools in saltmarshes of Gaspe, Quebec. Can. Field-Naturalist 123, 176–177.

Clausnitzer, V., Dijkstra, K.-D.B., Koch, R., Boudot, J.-P., Darwall, W.R.T., Kipping, J., Samraoui, B., Samways, M.J., Simaika, J.P., Suhling, F., 2012. Focus on African freshwaters: hotspots of dragonfly diversity and conservation concern. Front. Ecol. Environ. 10, 129–134.

Clausnitzer, V., Kalkman, V.J., Ram, M., Collen, B., Baillie, J.E.M., Bedjanič, M., Darwall, W.R.T., Dijkstra, K.-D.B., Dow, R., Hawking, J., Karube, H., Malikova, E., Paulson, D., Schütte, K., Suhling, F., Villanueva, R., von Ellenrieder, N., Wilson, K., 2009. Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. Biol. Conserv. 142, 1864–1869.

Conrad, K.F., Pritchard, G., 1992. An ecological classification of odonate mating systems: the relative influence of natural, inter- and intra-sexual selection on males. Biol. J. Linn. Soc. 45, 255–269.

Corbet, P.S., 1983. Odonata in Phytotelmata. In: Frank, J.H., Lounibos, L.P. (Eds.), Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities. Plexus Publishing, Medford, New Jersey, pp. 29–54.

Corbet, P.S., 1999. Dragonflies: Behaviour and Ecology of Odonata. Harley Books, Colchester.

Corbet, P.S., 2002. Stadia and growth ratios of Odonata: a review. Int. J. Odonatol. 5, 45–73.

Corbet, P.S., Suhling, F., Söndgerath, D., 2006. Voltinism of Odonata: a review. Int. J. Odonatol. 9, 1–44.

Cordero Rivera, A., Carballa, M.O.L., Utzeri, C., Vieira, V., 2005. Parthenogenetic *Ischnura hastata* (Say), widespread in the Azores (Zygoptera: Coenagrionidae). Odonatologica 34, 11–26.

Dijkstra, K-D.B., Bechly, G., Bybee, S.M., Dow, R.A., Dumont, H.J., Fleck, G., Garrison, R.W., Hämäläinen, M., Kalkman, V.J., Karube, H., May, M.L., Orr, A.G., Paulson, D., Rehn, A.C., Theischinger, G., Trueman, J.W.H., van Tol, J., von Ellenrieder, N., Ware, J., 2013. The classification and diversity of dragonflies and damselflies (Odonata). In: Zhang, Z-Q. (Ed.), Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness. Zootaxa, 3703, 036–045.

Dijkstra, K.-D.B., Kalkman, V.J., Dow, R.A., Vieira, V., Stokvis, F.R., Van Tol, J. 2014. Redefining the damselfly families: a comprehensive molecular phylogeny of Zygoptera (Odonata). Syst. Entomol. 39, 68–96.

Dijkstra, K.-D.B., Lempert, J., 2003. Odonate assemblages of running waters in the upper Guinean forest. Arch. Hydrobiol. 157, 397–412.

Dijkstra, K.-D.B., Kalkman, V.J., 2012. Phylogeny, classification and taxonomy of European dragonflies and damselflies (Odonata): a review. Org. Divers. Evol. 12, 209–227.

Dumont, H.J., Vierstraete, A., Vanfleteren, J.R., 2010. A molecular phylogeny of the Odonata (Insecta). Syst. Entomol. 35, 6–18.

Dunson, W.A., 1980. Adaptations of nymphs of a marine dragonfly, *Erythrodiplax berenice*, to wide variations in salinity. Physiol. Zool. 53, 445–452.

von Ellenrieder, N., 2002. A phylogenetic analysis of the extant Aeshnidae (Odonata: Anisoptera). Syst. Entomol. Lond. 27, 437–467.

Fincke, O., 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata, Coenagrionidae). Behav. Ecol. Sociobiol. 10, 293–302.

Fincke, O., 1999. Organization of predator assemblages in Neotropical tree holes: effects of biotic factors and priority. Ecol. Entomol. 24, 12–23.

Fincke, O.M., Tylczak, L.A., 2011. Effects of zebra mussel attachment on the foraging behaviour of a larval dragonfly, *Macromia illinoiensis*. Ecol. Entomol. 36, 760–767.

Fleck, G., Brenk, M., Misof, B., 2008a. Larval and molecular characters help to solve phylogenetic puzzles in the highly diverse dragonfly family Libellulidae (Insecta: Odonata: Anisoptera): the Tetrathemistinae are a polyphyletic group. Org. Divers. Evol. 8, 1–16.

Fleck, G., Ullrich, B., Brenk, M., Wallnisch, C., Orland, M., Bleidissel, S., Misof, B., 2008b. A phylogeny of anisopterous dragonflies (Insecta, Odonata) using mtRNA genes and mixed nucleotide/doublet models. J. Zool. Syst. Evol. Res. 46, 310–322.

Flenner, I., Richter, O., Suhling, F., 2010. Rising temperature and development in dragonfly populations at different latitude. Freshwater Biol. 55, 397–410.

Flenner, I., Sahlén, G., 2008. Dragonfly community re-organisation in boreal forest lakes: rapid species turnover driven by climate change? Insect Conserv. Diver. 1, 169–179.

Gorb, S., 1999. Serial elastic elements in the damselfly wing: mobile vein joints contain resilin. Naturwissenschaften 86, 552–555.

Gresens, S.E., Cothran, M.L., Thorp, J.H., 1982. The influence of temperature on the functional response of the dragonfly *Celithemis fasciata* (Odonata: Libellulidae). Oecologia 53, 281–284.

Haritonov, A., Popova, O., 2011. Spatial displacement of Odonata in south–west Siberia. Int. J. Odonatol. 14, 1–10.

Hassall, C., Thompson, D.J., 2008. The effects of environmental warming on Odonata: a review. Int. J. Odonatol. 11, 131–153.

Hoffmann, J., 2010. Do climate changes influence dispersal and population dynamics of dragonflies in the western Peruvian Andes? BioRisk 5, 47–72.

Horváth, Z., Ferenczi, M., Móra, A., Vad, C., Ambrus, A., Forró, L., Szövényi, G., Andrikovics, S., 2012. Invertebrate food sources for waterbirds provided by the reconstructed wetland of Nyirkai–Hany, northwestern Hungary. Hydrobiologia, 1–14.

Jacob, U., Walther, H., Klenke, R., 1984. Aquatic insect larvae as indicators of limiting minimal contents of dissolved oxygen – part II. Aquat. Insects 6, 185–190.

Jakob, C., Suhling, F., 1999. Risky times? Mortality during emergence in two species of dragonflies (Odonata: Gomphidae, Libellulidae). Aquat. Insects 21, 1–10.

Johansson, F., 1991. Foraging modes in an assemblage of odonate larvae – effects of prey and interference. Hydrobiologia 209, 79–87.

Johansson, F., 1993. Intraguild predation and cannibalism in odonate larvae: effects of foraging behaviour and zooplankton availability. Oikos 66, 80–87.

Johansson, F., Mikolajewski, D.J., 2008. Evolution of morphological defenses. In: Córdoba-Aguilar, A. (Ed.), Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research. Oxford University Press, pp. 70–74.

Johansson, F., Suhling, F., 2004. Behaviour and growth of dragonfly larvae along a permanent to temporary water habitat gradient. Ecol. Entomol. 29, 196–202.

Johnson, D.M., 1991. Behavioural ecology of larval dragonflies and damselflies. Trends Ecol. Evol. 6, 8–13.

Kalkman, V.J., Clausnitzer, V., Dijkstra, K.-D.B., Orr, A.G., Paulson, D.R., van Tol, J., 2008. Global diversity of dragonflies (Odonata) in freshwater. Hydrobiologia 595, 351–363.

Kalkman, V.J., Orr, A.G., 2012. The Australian monsoon tropics as a barrier for exchange of dragonflies (Insecta: Odonata) between New Guinea and Australia. Hydrobiologia 693, 55–70.

Karlsson, M., Sahlén, G., Koch, K., 2010. Continuous and stepwise oocyte production in Libellulidae (Anisoptera). Odonatologica 39, 107–119.

Kefford, B.J., Palmer, C.G., Nugegoda, D., 2005. Relative salinity tolerance of freshwater macroinvertebrates from the south-east Eastern Cape, South Africa compared with the Barwon Catchment, Victoria, Australia. Mar. Freshwater Res. 56, 163–171.

Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A., Holt, R.D., 2005. Trophic cascades across ecosystems. Nature 437, 880–883.

Krebs, J.R., Avery, M.I., 1984. Chick growth and prey quality in the European bee–eater (*Merops apiaster*). Oecologia 64, 363–368.

Krishnaraj, R., Pritchard, G., 1995. The influence of larval size, temperature, and components of the functional response to prey density on growth rates of the dragonflies *Lestes disjunctus* and *Coenagrion resolutum* (Insecta: Odonata). Can. J. Zool. 73, 1672–1680.

Kuitunen, K., Gorb, S.N., 2011. Effects of cuticle structure and crystalline wax coverage on the coloration in young and old males of *Calopteryx splendens* and *C. virgo*. Zoology 114, 129–139.

Martens, A., 1996. Die Federlibellen Europas: Platycnemididae. Westarp Wissenschaften, Magdeburg.

Matushkina, N.A., Lambret, P.H., 2011. Ovipositor morphology and egg laying behaviour in the dragonfly *Lestes macrostigma* (Zygoptera: Lestidae). Int. J. Odonatol. 14, 69–82.

May, M.L., 1976. Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). Ecol. Monogr. 46, 1–32.

McPeek, M.A., 2000. Predisposed to adapt? Clade-level differences in characters affecting swimming performance in damselflies. Evolution 54, 2072–2080.

Meyer, E.P., Lebhart, T., 1993. Morphological specializations of dorsal rim ommatidia in the compound eye of dragonflies and damselflies (Odonata). Cell. Tissue Res. 272, 17–22.

Miller, P.L., 1964. Notes on *Ictinogomphus ferox* Rambur (Odonata, Gomphidae). The Entomologist 97, 52–66.

Miller, P.L., 1992. The effect of oxygen lack on egg hatching in an Indian dragonfly, *Potamarcha congener*. Physiol. Entomol. 17, 68–72.

Miller, P.L., 1995. Dragonflies. Richmond Publishing, Slough.

Norling, U., 1984. Photoperiodic control of larval development in *Leucorrhina dubia* (Vander Linden): a comparison between populations from Northern and Southern Sweden (Anisoptera: Libellulidae). Odonatologica 13, 529–550.

Olberg, R.M., Worthington, A.H., Venator, K.R., 2000. Prey pursuit and interception in dragonflies. J. Comp. Physiol. A 186, 155–162.

Olberg, R.M., Worthington, A.H., Fox, J.L., Bessette, C.E., Loosemore, M.P., 2005. Prey size selection and distance estimation in foraging adult dragonflies. J. Comp. Physiol. A 191, 791–797.

Oppel, S., 2005. Habitat associations of an Odonata community in a lower montane rainforest in Papua New Guinea. Int. J. Odonatol. 8, 243–257.

Orr, A.G., 1994. Life histories and ecology of Odonata breeding in phytotelmata in Bornean rainforest. Odonatologica 23, 365–377.

Orr, A.G., 2006. Odonata in Bornean tropical rain forest formations: diversity, endemicity and implications for conservation management. In: Cordero Rivera, A. (Ed.), Forest and Dragonflies. Pensoft Publishers, Sofia, pp. 51–78.

Ott, J., 2010. Dragonflies and climatic change – recent trends in Germany and Europe. BioRisk 5, 253–286.

Padeffke, T., Suhling, F., 2003. Temporal priority and intraguild predation in temporary waters: an experimental study using Namibian desert dragonflies. Ecol. Entomol. 28, 340–347.

Pickup, J., Thompson, D.J., 1984. The effects of prey density on development of larvae of the damselfly *Lestes sponsa* (Hans.) (Zygoptera: Lestidae). Adv. Odonatol. 2, 169–176.

Pierce, C.L., 1988. Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. Oecologia 77, 81–90.

Pritchard, G., 1965. Prey capture by dragonfly larvae. Can. J. Zool. 43, 271–289.

Pritchard, G., Harder, L.D., Mutch, R.A., 1996. Development of aquatic insect eggs in relation to temperature and strategies for dealing with different thermal environments. Biol. J. Linn. Soc. 58, 221–244.

Prum, R.O., Cole, J.A., Torres, R.H., 2004. Blue integumentary structural colours in dragonflies (Odonata) are not produced by incoherent Tyndall scattering. J. Exp. Biol. 207, 3999–4009.

Punzo, F., 1988. Effects of low environmental pH and temperature on hatching and metabolic rates in embryos of *Anax junius* Drury (Odonata: Aeshnidae) and the role of hypoxia in the hatching process. Comp. Biochem. Physiol. 91, 333–336.

Raebel, E.M., Merckx, T., Riordan, P., Macdonald, D.W., Thompson, D.J., 2010. The dragonfly delusion: why it is essential to sample exuviae to avoid biased surveys. J. Insect Conserv. 14, 523–533.

Rebora, M., Salerno, G., Piersanti, S., Dell'Otto, A., Gaino, E., 2012. Olfaction in dragonflies: electrophysiological evidence. J. Insect Physiol. 58, 270–277.

Rehfeldt, G.-E., 1992. Impact of predation by spiders on a territorial damselfly (Odonata: Calopterygidae). Oecologia 89, 550–556.

Rehn, A.C., 2003. Phylogenetic analysis of higher-level relationships of Odonata. Syst. Entomol. 28, 181–239.

Remsburg, A.J., Olson, A.C., Samways, M.J., 2008. Shade alone reduces adult dragonfly (Odonata: Libellulidae) abundance. J. Insect Behav. 21, 460–468.

Rolff, J., 2001. Evolutionary ecology of water mite-insect interactions: a critical appraisal. Arch. Hydrobiol. 152, 353–358.

Rowe, R., 1987. The Dragonflies of New Zealand. Auckland University Press, Auckland.

Rüppell, G., 1989. Kinematic analysis of symmetrical flight manoeuvres of Odonata. J. Exp. Biol. 144, 13–42.

Sahlén, G., 1995. The insect eggshell. Ultrastructure, organisation, and adaptive traits in Odonata and Diptera. Acta Univ. Ups. 111, 1–27.

Samraoui, F., Nedjah, R., Boucheker, A., Alfarhan, A.H., Samraoui, B., 2012. Patterns of resource partitioning by nesting herons and ibis: how are Odonata exploited? Comptes Rendus Biol. 335, 310–317.

Samways, M.J., Sharratt, N.J., Simaika, J.P., 2010. Effect of alien riparian vegetation and its removal on a highly endemic river macroinvertebrate community. Biol. Invasions 13, 1305–1324.

Sherk, T.E., 1977. Development of the compound eyes of dragonflies (Odonata). I. Larval compound eyes. J. Exp. Zool. 201, 391–416.

Sherk, T.E., 1978a. Development of the compound eyes of Dragonflies (Odonata). II. Development of the larval compound eyes. J. Exp. Zool. 203, 47–60.

Sherk, T.E., 1978b. Development of the compound eyes of dragonflies (Odonata). III. Adult compound eyes. J. Exp. Zool. 203, 61–80.

Sherrat, T.N., Hassall, C., Laird, R.A., Thompson, D.J., Cordero-Rivera, A., 2011. A comparative analysis of senescence in adult damselflies and dragonflies (Odonata). J. Evol. Biol. 24, 810–822.

Simaika, J.P., Samways, M.J., 2009. An easy-to-use index of ecological integrity for prioritizing freshwater sites and for assessing habitat quality. Biodivers. Conserv. 18, 1171–1185.

Sternberg, K., 1990. Autökologie von sechs Libellenarten der Moore und Hochmoore des Schwarzwaldes und Ursachen ihrer Moorbindung (Dissertation). Albert-Ludwigs-Universität, Freiburg.

Sternberg, K., 1995. Influence of oviposition date and temperature upon embryonic development in Somatochlora alpestris and S. arctica (Odonata: Corduliidae). J. Zool. Lond. 235, 163–174.

Stoks, R., 1999. Effect of lamellae autotomy on survival and foraging success of the damselfly Lestes sponsa (Odonata: Lestidae). Oecologia 117, 443–448.

Stoks, R., De Block, M., McPeek, M.A., 2005. Alternative growth and energy storage responses to mortality threats in damselflies. Ecol. Lett. 8, 1307–1316.

Stoks, R., McPeek, M.A., 2003. Predators and life histories shape Lestes damselfly assemblages along a freshwater habitat gradient. Ecology 84, 1576–1587.

Suhling, F., 1995. Temporal patterns of emergence of the riverine dragonfly Onychogomphus uncatus (Odonata: Gomphidae). Hydrobiologia 302, 113–118.

Suhling, F., Martens, A., 2007. Dragonflies and Damselflies of Namibia. Gamsberg Macmillan, Windhoek.

Suhling, F., Müller, O., 1996. Die Flußjungfern Europas (Gomphidae). Westarp, Magdeburg und Spektrum, Heidelberg.

Suhling, F., Sahlén, G., Kasperski, J., Gaedecke, D., 2005. Behavioural and life history traits in temporary and perennial waters: comparisons among three pairs of sibling dragonfly species. Oikos 108, 609–617.

Suhling, F., Schenk, K., Padeffke, T., Martens, A., 2004. A field study of larval development in a dragonfly assemblage in African desert ponds (Odonata). Hydrobiologia 528, 75–85.

Suhonen, J., Suutari, E., Kaunisto, K., Krams, I., 2012. Patch area of macrophyte Stratiotes aloides as a critical resource for declining dragonfly Aeshna viridis. J. Insect Conserv. 17, 393–398.

Thompson, D.J., 1987. Regulation of damselfly populations: the effects of weed density on larval mortality due to predation. Freshwater Biol. 17, 367–371.

Thomsen, P.F., Kielgast, J., Iversen, L.L., Wiuf, C., Rasmussen, M., Thomas, M., Gilbert, P., Orlando, L., Willerslev, E., 2011. Monitoring endangered freshwater biodiversity using environmental DNA. Mol. Ecol. 21, 2565–2573.

Tillyard, R.J., 1917. The Biology of Dragonflies. University Press, Cambridge.

Tol, J. van, 2012. Odonata: catalogue of the Odonata of the World. Dec. 2011 version. In: Bisby, F., Roskov, Y., Culham, A., Orrell, T., Nicolson, D., Paglinawan, L., Bailly, N., Appeltans, W., Kirk, P., Bourgoin, T., Baillargeon, G., Ouvrard, D. (Eds.), Species 2000 & ITIS, 2012 Annual Checklist. Species 2000, Reading, UK (DVD edition).

Trueman, J.W.H., 1990. Eggshells of Australian Gomphidae: plastron respiration in eggs of stream-dwelling Odonata. Odonatologica 19, 395–401.

Van Buskirk, J., 1989. Density-dependent cannibalism in larval dragonflies. Ecology 70, 1442–1449.

Waage, J.K., 1979. Dual function of the damselfly penis: sperm removal and transfer. Science 203, 916–918.

Ware, J., May, M., Kjer, K., 2007. Phylogeny of the higher Libelluloidea (Anisoptera: Odonata): an exploration of the most speciose superfamily of dragonflies. Mol. Phylogenet. Evol. 45, 289–310.

Watts, P.C., Rousset, F., Saccheri, I.J., Leblois, R., Kemp, S.J., Thompson, D.J., 2007. Compatible genetic and ecological estimates of dispersal rates in insect (Coenagrion mercuriale: Odonata: Zygoptera) populations: analysis of 'neighbourhood size' using a more precise estimator. Mol. Ecol. 16, 737–751.

Wikelski, M., Moskowitz, D., Adelman, J.S., Cochran, J., Wilcove, D.S., . May, M.L., 2006. Simple rules guide dragonfly migration. Biol. Lett. 2, 325–329.

Wildermuth, H., 1994. Habitatselektion bei Libellen. Adv. Odonatol. 6, 223–257.

Wildermuth, H., 2000. Totstellreflex bei Großlibellenlarven (Odonata). Libellula 19, 17–39.

Wildermuth, H., Martens, A., 2007. The feeding action of Forcipomyia paludis (Diptera: Ceratopogonidae), a parasite of Odonata imagines. Int. J. Odonatol. 10, 249–255 (pl IV).

Wilson, K., 2009. Dragonfly giants. Agrion 13, 29–31.

Wissinger, S.A., 1992. Niche overlap and the potential for competition and intraguild predation between size-structured populations. Ecology 73, 1431–1444.

Wohlfahrt, B., Mikolajewski, D.J., Joop, G., Suhling, F., 2005. Are behavioural traits in prey sensitive to the risk imposed by predatory fish? Freshwater Biol. 51, 76–84.